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Burrowing lobsters mostly from shallow coastal environments in Papua New Guinea (Crustacea: Axiidea: Axiidae, Micheleidae)

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Abstract

Poore, G.C.B. 2018. Burrowing lobsters from shallow coastal environments in Papua New Guinea (Crustacea: Axiidea: Axiidae, Micheleidae). *Memoirs of Museum Victoria* 77: 1–14.

Surveys of coral reefs and associated habitats have discovered nine species of Axiidae and one of Micheleidae in Papua New Guinea. Only the micheleid is new to science. The collection provides an opportunity to provide colour photographs of some and to revisit their taxonomy. Two species are synonymised with others: *Alienaxiopsis lizardensis* Sakai, 2011 with *A. clypeata* (De Man, 1905) and *Allaxiopsis bougainvillensis* Sakai, 2011 with *Axiopsis picteti* var. *spiniimana* De Man, 1905, now *Allaxiopsis spiniimana* (De Man, 1905). *Axiopsis pica* Kensley, 2003 is recognised as distinct from *A. serratifrons*, with which it co-occurs. *Michelea papua* sp. nov. is described as new.

Keywords

Crustacea, Axiidae, Micheleidae, *Alienaxiopsis*, *Allaxiopsis*, *Axiopsis*, *Parascytoleptus*, *Paraxiopsis*, *Ralumcaris*, *Michelea*, Papua New Guinea, taxonomy

Introduction

The Our Planet Reviewed (La Planète revisitée) expeditions in Papua New Guinea in 2012 and 2014, coordinated by Philippe Bouchet for the Muséum nationale d'Histoire naturelle, Paris, discovered a diverse fauna of axiidean ghost shrimps and burrowing lobsters in shallow water. Ghost shrimps of the family Callinassidae are being studied separately, but here burrowing lobsters belonging to Axiidae and Micheleidae are dealt with.

While only one of the ten species recorded is new, four are first records for Papua New Guinea and provide new morphological information that illuminates the complicated and sometimes confusing taxonomy of some species. Seven species were photographed in colour. The discoveries have provided information for a reassessment of genera of Axiidea (work in progress) that were most recently reviewed (as Axiidea) by Sakai (2011).

The material comes from two sampling series in shallow water environments in Papua New Guinea using a variety of methods, including divers in shallow water brushing coral rubble under water (PB and KB prefixes), hand-dredging (PD and KD prefixes) or sampling individually by hand (PR, KR and KZ prefixes). The expedition in November–December 2012 near Madang, Madang Province, provided samples in the PAPUA NIUGINI series. The expedition in April 2014 based in Kavieng, New Ireland, provided samples in the KAVIENG 2014 series. These collections were augmented for comparative purposes with others from shallow waters of Papua New Guinea in other museums, and by material from the Kimberley region of Western Australia.

Material and methods

Material is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN, IU-prefixes), Museum für Naturkunde, Berlin (ZMB), Zoological Museum, Hamburg (ZMH), Museums Victoria, Melbourne (NMV), the Australian Museum, Sydney (AM), Western Australian Museum, Perth (WAM) and Northern Territory Museum and Art Gallery, Darwin (NTMAG). All measurements are of carapace length (cl.) including rostrum. Photographs of fresh specimens that were taken in the lab shortly after collection were made by Tin-Yam Chan (TYC) and Arthur Anker (AA).

Results

Four of the ten species recorded, *Alienaxiopsis clypeata* (De Man, 1888), *Allaxiopsis spiniimana* (De Man, 1905), *Axiopsis pica* Kensley, 2003, and *Paraxiopsis austrinus* Sakai, 1994, have been recorded from Papua New Guinea for the first time. *Axiopsis* (*Axiopsis*) *pitatucensis* De Man, 1925 (= *Calaxius pitatucensis*), described from Papua New Guinea, was not collected but is probably a higher water species. It is surprising that, despite hundreds of dredge and diving samples targeting axiidean habitats in shallow water, more species were not captured. Most of the species found are widespread in the Indo West-Pacific; in particular, *Axiopsis serratifrons* and *Paraxiopsis brocki* have been recorded numerous times from many places. The possibility that these last two are species complexes cannot be discounted.

Infraorder Axiidea de Saint Laurent, 1979

Axiidae Huxley, 1879

Alienaxiopsis Sakai, 2011

Alienaxiopsis Sakai, 2011: 32–33.

Type species. *Alienaxiopsis lizardensis* Sakai, 2011, by original designation.

Remarks. *Alienaxiopsis* was erected to include two species, *Alienaxiopsis lizardensis* Sakai, 2011 (type species) and *A. clypeata* (De Man, 1888). Sakai's (2011) key differentiated the two species but, as explained below, the two are synonymous.

Alienaxiopsis clypeata (De Man, 1888)

Figs 1a, b, 3

Axiis clypeatus De Man, 1888: 470, pl. 20 fig. 2.

Axiopsis (*Axiopsis*) *clypeata*.—De Man, 1925: 70.

Allaxius clypeatus.—Sakai and de Saint Laurent, 1989: 73–74.—Poore and Collins, 2009: 237.

Alienaxiopsis lizardensis Sakai, 2011: 34–36, fig. 2. Syn. nov.

Material examined. Papua New Guinea. Madang Province. PAPUA NIUGINI stations. Tab I., 05° 09.9' S, 145° 50.4' E, 20 m (stn PB06), IU-2013-7096 (ovigerous female, 3.4 mm).

New Ireland Province, Kavieng lagoon, KAVIENG 2014 stations. E side of Ral I., 02° 36.7' S, 150° 42.6' E, 3–10 m (KZ22), IU-2014-1142 (ovigerous female, 2.5 mm; male, 4.2 mm). Mouth of Albatross Passage, E side, 02° 35.2' S, 150° 43.1' E, 13 m (KB72), NMV J71641 (female, 4.2 mm). New Ireland mainland, N coast, 02° 35.2' S, 150° 50.3' E, 17 m (KB66), IU-2016-8134 (female, 3.5 mm).

Australia. Queensland, Great Barrier Reef, Yonge Reef, near Lizard I., 14° 38' S, 145° 38' E, AM P.25014 (holotype of *Alienaxiopsis lizardensis*, male, 4.7 mm).

Photographed specimens not seen. Papua New Guinea. Madang Province. PAPUA NIUGINI stations: location not specified, 15 m (stn PR89), 1 specimen. Kranket I., 05° 12' S, 145° 48.8' E (stn PR86), 2 ovigerous females.

Type locality. Ambon, Indonesia.

Supplementary description. Rostrum acute, depressed, 0.3 length of rostral base–cervical groove, with pair of erect lateral spines at midpoint and larger pair at base. Median gastric carina obsolete, with 1 tooth, ending in broad triangular plate; submedian gastric carina obsolete, with 2 erect teeth; supraocular spine oblique, not marginal; lateral gastric carina obsolete, with 1 erect tooth. Eyestalk reaching end of rostrum. Antenna article 2 with broadly triangular distal spine; scaphocerite 5 times as long as greatest height (lateral view), reaching to midpoint of article 5. Major cheliped ischium, merus and carpus each with minute distal tooth on lower margin; propodus swollen, upper margin 1.35 times greatest height, carinate, with distal tooth; fixed finger 0.5 times length of upper margin of propodus, with blunt distal tooth near tip of cutting edge; dactylus 2.3 times as long as wide, cutting edge with 2 low rounded teeth in proximal half. Minor cheliped as long as major cheliped, propodus about 0.75 times as high as on major cheliped; ischium and merus each with minute distal

tooth on lower margin; propodus swollen, upper margin 1.2 times greatest height, carinate, with distal tooth; fixed finger as long as upper margin of propodus, with distal tooth on cutting edge; dactylus 3.2 times as long as wide, cutting edge smooth. Telson 1.1 times as wide as long at level of most anterior lateral teeth; distal margin 0.5 times telson greatest width; lateral margin with 4 teeth; distal margin convex, with 1 or 2 lateral articulating robust setae, with median spine; face with 2 pairs of spines. Uropodal endopod twice as long as wide; anterior margin strongly lobed proximally (as rounded shoulder), otherwise concave with strong tooth at midpoint and elevated distal spine; posterior margin convex, unarmed; distal margin straight, oblique, with strong elevated spine at anterior end, smaller spine at posterior end; facial rib with 3 spines. Uropodal exopod oval, twice as long as wide; anterior margin of article 1 with 4 teeth; posterior margin convex; distal margin irregular, 3 marginal spines, stronger spine defining posterior corner, strong articulating spine near anterior corner; article 2 oval, with distal spine almost as long as body of article.

Colour. Translucent with bright red band anteriorly and dorsolaterally on carapace, dorsolaterally on pleon, and on upper margins of cheliped carpus and propodus; maxilliped 3 bright red; cheliped fingers white.

Distribution. Indo-West Pacific (Guam, Papua New Guinea, Indonesia, Fiji); to 20 m depth.

Remarks. De Man's (1888) description was extensive but his drawings few. Here, colour photographs and figures of the carapace, pereopods 1 and tail fan are included.

Sakai (2011) based a new species *Alienaxiopsis lizardensis* on the specimen from Lizard I., Great Barrier Reef, Australia (AM P.25014) that was examined and identified by Poore and Collins (2009) as *Allaxius clypeatus*. Sakai listed Poore and Collins' record under the synonymy and distribution of both species. This specimen has been re-examined and redrawn; no differences in the gastric ornamentation (characters alleged to differentiate the two) could be detected between it, material from Papua New Guinea or De Man's (1888) figures. Sakai's (2011: fig. 2B) figure of the dorsal carapace is quite misleading. *Alienaxiopsis lizardensis* is here synonymised with *A. clypeata*.

Until now, *Alienaxiopsis clypeata* was known only from Ambon, Indonesia (type locality), Guam and Fiji (Kensley, 2003), but is here recorded from Papua New Guinea. The record from Fiji is based on unpublished data from the USNM online database <http://collections.nmnh.si.edu/search/iz/>.

Allaxiopsis Sakai, 2011

Allaxiopsis Sakai, 2011: 34–35.

Remarks. Sakai (2011) included three species in *Allaxiopsis* but confused their records. The type species, *Paraxius picteti* Zehntner, 1894, was described from a single female (cl. 10 mm) collected at Ambon, Indonesia. Two males (the larger cl. 8.5 mm) were recorded from *Siboga* station 209 at Kabaena I., Indonesia, by De Man (1905) and then re-illustrated (De Man, 1925). More specimens were recorded from Guam, Marshall Islands, and Fiji by Kensley (2003). *Allaxiopsis spinimana* (De

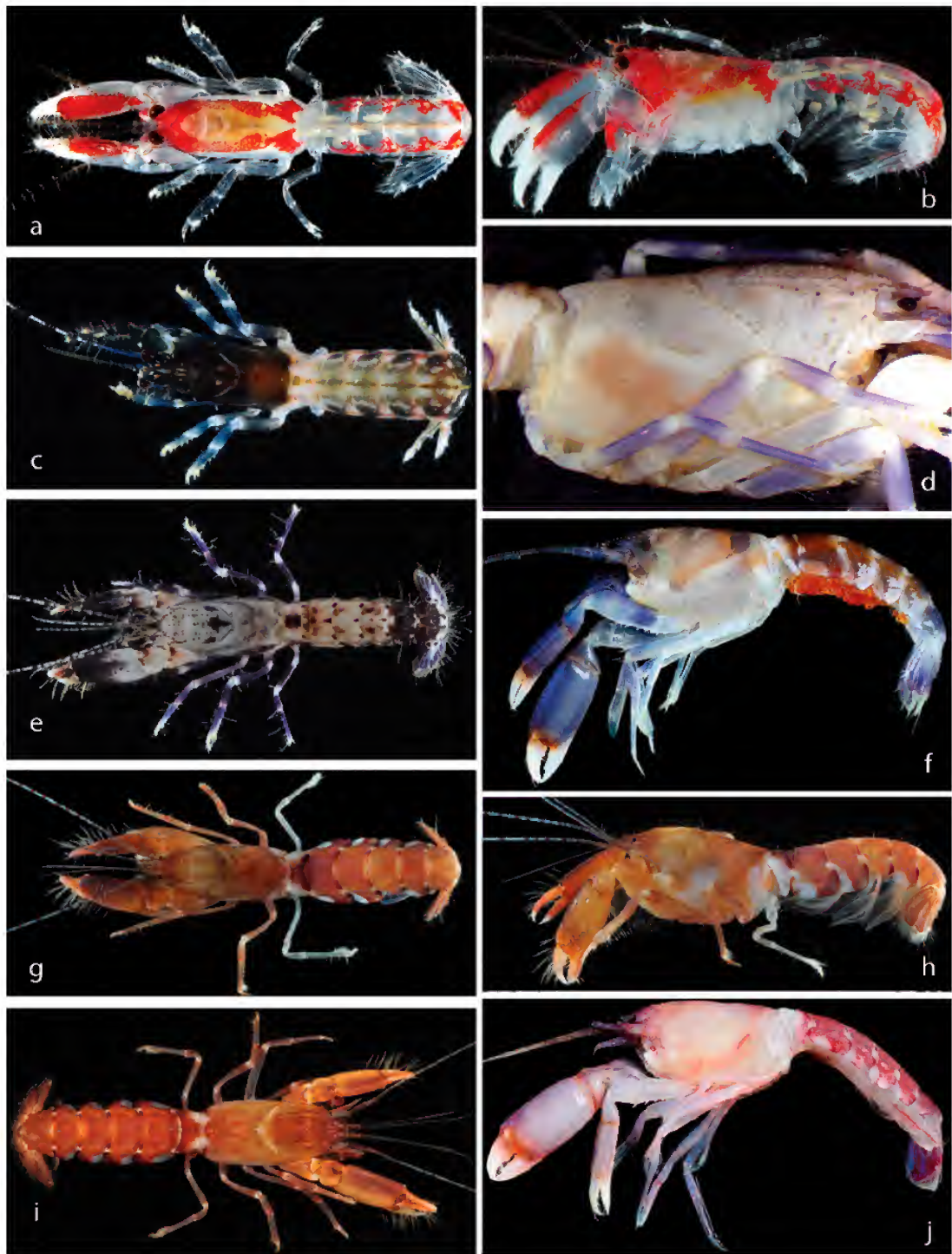


Figure 1. *Alienaxiopsis clypeata* (De Man, 1888): a, b, MNHN unregistered (stn PR86). *Allaxiopsis picteti* (Zehntner, 1894): c, MNHN IU-2013-1209. *Axiopsis pica* Kensley, 2003, MNHN IU-2013-7048: d, preserved; e, living. *Axiopsis serratifrons* A. Milne-Edwards, 1873: f, MNHN IU-2013-638; g, h, MNHN IU-2013-7052; i, MNHN IU-2013-7046; j, MNHN IU-2013-302. Photo credits: AA, a–c, e, g–j; TYC, f; GCBP, d.



Figure 2. *Parascytoleptus papua* Poore and Collins, 2010: a, MNHN IU-2014-2735; b, MNHN IU-2013-7128. *Paraxiopsis brocki* (De Man, 1888): c, MNHN IU-2013-7108; d, MNHN IU-2014-2736. *Ralumcaris bisquamosa* (De Man, 1905): e, MNHN IU-2013-7120. Photo credits: AA, b, c, e; TYC, a, d.

Man, 1905) was originally described as a variety of *A. picteti* from *Siboga* station 209 based on a 9.25 mm female and a smaller male. The variety was treated at the species level by Sakai and de Saint Laurent (1989) and has been rediscovered (see below). *Allaxiopsis bougainvillensis* Sakai, 2011 (type species of the genus) was described from much smaller specimens (4.5 mm and 4.9 mm) from Bougainville, Papua New Guinea and is treated here as a synonym of *A. spinimana*. Sakai included Kabaena I., Sulawesi, Indonesia, in the distribution of all three species and as type locality of the last two, contradicting the data provided with his type specimens. Each of the two species is diagnosed here with a minimal character suite.

Allaxiopsis picteti (Zehntner, 1894)

Figs 1c, 4

Paraxius picteti Zehntner, 1894: 196–199, pl. 9 fig. 25.

?*Axiopsis picteti*.—Borradaile, 1903: 539.

Axiopsis (*Axiopsis*) *picteti*.—De Man, 1925: 6, 70, 92–96, pl. 7 fig. 16.

Allaxius picteti.—Sakai and de Saint Laurent, 1989: 75.—Kensley, 2003: 361, pls 5, 6.

Allaxiopsis picteti.—Sakai, 2011: 39–40.

Material examined. Papua New Guinea. Madang Province. PAPUA NIUGINI stations. S of Urembo I., outer slope, 05° 15.9' S, 145° 47.1' E, 3 m (stn PB43), IU-2013-1209 (male, 8.3 mm). N of Bil Bil I., 05° 17.7' S, 145° 46.9' E, 5 m (stn PB51), IU-2013-7014 (male, 2.5 mm).

New Ireland Province. Kavieng lagoon, KAVIENG 2014 stations. S side of Patio I., 02° 36.2' S, 150° 31.6' E, 6–8 m (stn KB38), IU-2014-2526 (male, 6.8 mm). NW point of Nusa I., 02° 33.9' S, 150° 46.7' E, 8–10 m (stn KS3), IU-2014-2041 (female, 2.0 mm).

Australia. Western Australia, Kimberleys, Echuca Shoal, <23 m, 13° 53.781' S, 123° 53.686' E (Woodside Kimberley Survey stn 107/ K12), WAM C50773 (female, 5.5 mm).

Type locality. Ambon, Indonesia.

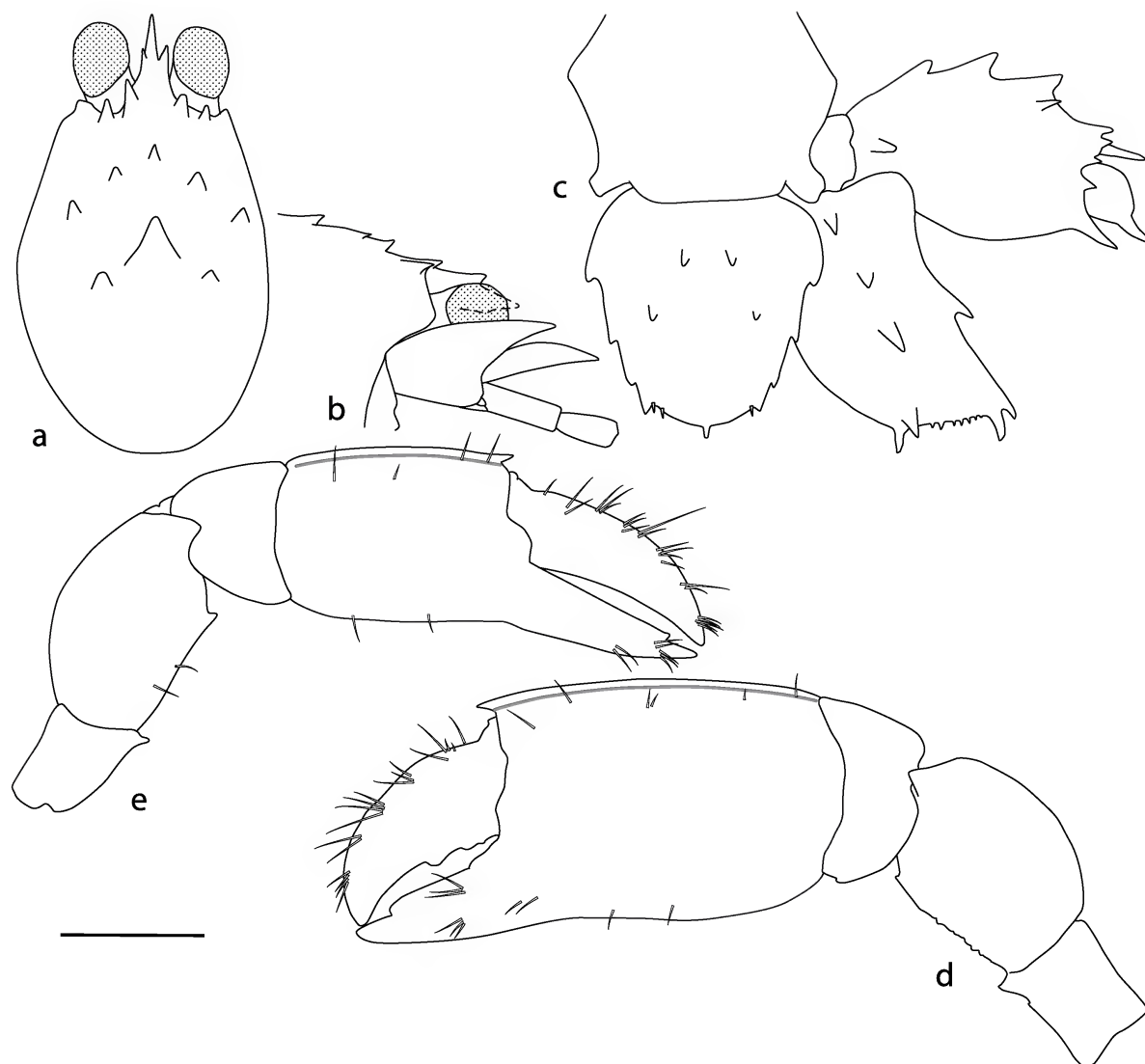


Figure 3. *Alienaxiopsis clypeata* (De Man, 1888), male, MNHN IU-2016-8134: a, b, anterior carapace, dorsal and lateral views; c, telson and uropod; d, major left cheliped; e, minor right cheliped. Scale bar = 1 mm.

Diagnosis. Major cheliped, propodus with blunt tubercles on lateral and mesial faces, more prominent nearer upper margin. Minor cheliped, propodus tuberculate on lateral and mesial faces.

Supplementary description. Rostrum acute, depressed, 0.3 length of rostral base–cervical groove, with pair of erect lateral spines near apex and larger pair at base. Gastric carina difficult to differentiate; median gastric carina obsolete except near base of rostrum, with sequence of 1, 1, 2, 2, 2 teeth; submedian gastric carina obsolete, with 1 tooth anteriorly and 2 or 3 teeth posteriorly; supraocular spine oblique, not marginal; lateral gastric carina with 2 or 3 blunt teeth. Eyestalk reaching beyond end of rostrum.

Antenna article 2 with small distal spine; scaphocerite 4 times as long as greatest height (lateral view), reaching third length of article 4. Major cheliped coxa–carpus unarmed; propodus upper margin 1.4 times greatest height, carinate, with 5 spines, lateral face tuberculate proximally near upper margin; fixed finger 0.5 times length of upper margin of propodus, cutting edge with 2 blunt distal teeth; dactylus cutting edge with 3 low rounded teeth in proximal half. Minor cheliped coxa–carpus unarmed; propodus upper margin 1.5 times greatest height, carinate, with 2 distal spines, lateral face with few proximal tubercles; fixed finger almost as long as upper margin of propodus, with distal teeth near

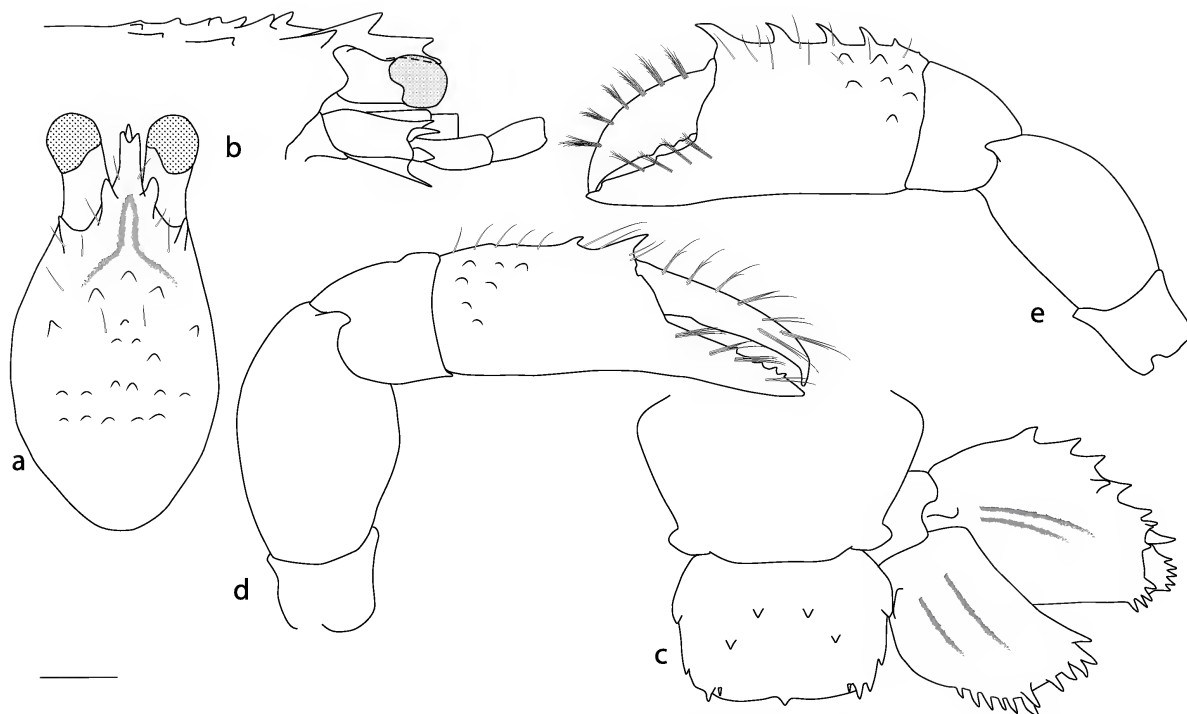


Figure 4. *Allaxiopsis picteti* (Zehntner, 1894), males, MNHN IU-2013-1209: a, b, anterior carapace, dorsal and lateral views; c, telson and uropod; d, minor right cheliped. MNHN IU-2013-2526: e, major left cheliped. Scale bar = 1 mm.

tip of cutting edge; dactylus cutting edge smooth. Telson 1.4 times as wide as long at level of most anterior lateral teeth; distal margin 0.8 times telson greatest width; lateral margin with 3 teeth; distal margin straight, with 1 lateral articulating robust seta, lateral fixed spine, with median spine; face with 2 pairs of spines. Uropodal endopod 1.6 times as long as wide; anterior margin strongly lobed proximally (as rounded shoulder), otherwise concave with or without spine at midpoint, with subdistal and distal spine; posterior margin convex, with 5 spines along distal third; distal margin straight, transverse, with depressed spine at anterior end, 2 marginal spines, 1 stronger spine and another superior, at posterior end; facial rib unarmed. Uropodal exopod semicircular, 1.5 times as long as wide; anterior margin of article 1 convex, with 5 or 6 marginal teeth, 1 submarginal; posterior margin straight, with 3 distal spines set obliquely; distal margin transverse, 3 marginal spines, strong articulating spine near anterior corner; article 2 with 5 teeth along distal margin.

Colour. Carapace high red-brown; pleon with patches of green-brown and scattered red chromatophores; antennal flagellum with alternating white and brown stripes; cheliped high blue; pereopods with transverse blue bands on major articles, otherwise white.

Distribution. Indonesia: Ambon (type locality), Kabaena I., Sulawesi (De Man, 1925); Guam; Marshall Islands; Fiji (Kensley, 2003); Papua New Guinea: Madang, Bougainville, New Ireland; Australia, N Western Australia; 3–20 m depth.

Remarks. Kensley (2003) reported on material from Guam and included a photograph with colours similar to the one here. Kensley also reported on unpublished records of the species from Papua New Guinea, Fiji and the Marshall Islands identified by him (see USNM online database <http://collections.nmnh.si.edu/search/iz/>). Kensley's record of the species from Malaysia is not on the database. The carapace, tail fan and the never-before-illustrated chelipeds are figured here.

Allaxiopsis spinimana (De Man, 1905)

Fig. 5

Axiopsis Picteti var. *spinimana* De Man, 1905: 597.

Axiopsis (Axiopsis) Picteti var. *spinimana*.—De Man, 1925: 6, 70, 96, pl. 7 fig. 17.

Allaxius spinimanus.—Sakai and de Saint Laurent, 1989: 75.

Allaxiopsis spinimana.—Sakai, 2011: 40.

Allaxiopsis bougainvillensis Sakai, 2011: 37–39, fig. 3. **Syn. nov.**

Material examined. Papua New Guinea. Bougainville, Teop I., 05° 34.3' S, 155° 4.7' E, (as 'Tiop Bougainville, German New Guinea', H. Schoede, ZMB 14440 (holotype female, 4.9 mm; paratype female, 4.5 mm of *Allaxiopsis bougainvillensis* Sakai, 2011) (both photographed by C.O. Coleman).

Madang Province, Channel between Pik I. and Kranket I., 05° 09.6' S, 145° 49.7' E, 3–8 m, coll. R. Hanley, NMV J67992 (2 ovigerous females, 7.5, 7.8 mm; 3 males, 3.2–5.0 mm; part of larger collection, NTMAG Cr.0100212).

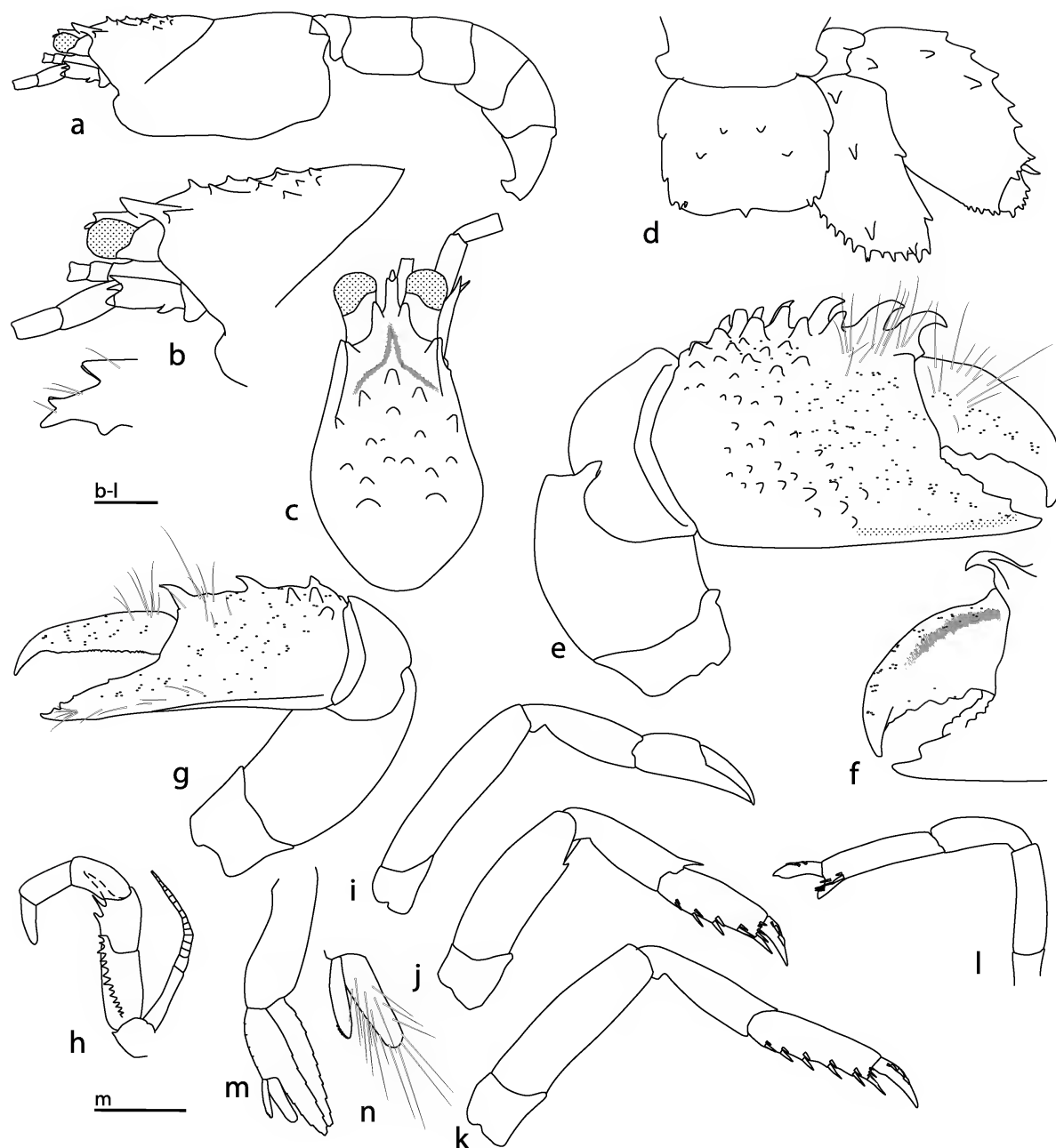


Figure 5. *Allaxiopsis spinimana* (De Man, 1905) male, NMV J67992: a, habitus; b, c, anterior carapace, dorsal and lateral views, with detail of rostrum; d, telson and uropod; e, major right cheliped, lateral; f, major right cheliped, fingers, mesial; g, minor left cheliped; h, maxilliped 3; i–l, pereopods 2–5; m, n, pleopod 2, with details of appendices interna and masculina. Scale bars = 1 mm. Bases of many setae indicated by small ovals.

Type locality. Indonesia, off south point of Kabaena I., 22 m (*Siboga* stn 209).

Diagnosis. Major cheliped, propodus with blunt tubercles on proximal lateral face, more prominent nearer upper margin becoming spine-like and more hooked towards distal upper margin. Minor cheliped, propodus with few tubercles on proximal lateral face, upper margin with 3 spines.

Supplementary description. Rostrum acute, depressed, 0.3 length of rostral base–cervical groove, with pair of erect lateral spines near apex, larger pair at midpoint, and ventral tubercle. Gastric carina difficult to differentiate; median gastric carina obsolete except near base of rostrum, with sequence of 1, 1, 2 teeth; submedian gastric carina obsolete, with 1 tooth anteriorly and 2 or 3 teeth posteriorly; supraocular spine oblique, not marginal; lateral gastric carina, with 2 blunt teeth. Eyestalk reaching beyond end of rostrum. Antenna article 2 with small distal spine; scaphocerite 4 times as long as greatest height (lateral view), reaching sixth length of article 4. Major cheliped ischium, merus and carpus each smooth on lower margin; propodus swollen, lateral face tuberculate over proximal half, tubercles larger closer to upper margin, upper margin about equal to greatest height, with 2 rows each of 6 spines, the larger ones sharper and more hooked distally; fixed finger 0.45 times length of upper margin of propodus, with 2 blunt distal teeth along cutting edge, with short tuberculate mesial ridge; dactylus 2.1 times as long as wide, with lateral carina near upper margin, cutting edge with 2 low rounded teeth in proximal half. Minor cheliped as long as major cheliped, propodus about 0.5 times as high as on major cheliped; ischium and merus smooth on lower margin; propodus swollen, propodus upper margin 1.5 times greatest height, lateral face with 3 tubercles on proximal lateral face, upper margin with 3 teeth, second and third sharp; fixed finger almost as long as upper margin of propodus, with 2 distal teeth on cutting edge; dactylus 4 times as long as wide, cutting edge smooth. Telson 1.4 times as wide as long at level of most anterior lateral teeth; distal margin 0.8 times telson greatest width; lateral margin with 3 teeth; distal margin excavate, with 1 lateral articulating robust seta, lateral fixed spine, with median spine; face with 2 pairs of spines. Male pleopod 2 appendix masculina 1.3 times as long as appendix interna, stiff setae on posterior face. Uropodal endopod 1.8 times as long as wide; anterior margin strong lobed proximally (as rounded shoulder), otherwise concave with spine at midpoint, with subdistal and distal spine; posterior distal margin curved, with 10 spines, the most distal 2 submarginal, anterodistal angle marked by 2 spines; facial rib with 3 spines. Uropodal exopod semicircular, 1.8 times as long as wide; anterior margin of article 1 convex, with 6 marginal teeth; posterior margin straight, with 5 distal spines set obliquely; distal margin transverse, 2 marginal spines, strong articulating spine near anterior corner, facial rib with 3 spines; article 2 with 5 teeth along distal margin.

Colour. Traces of purple on pereopod 1 propodus and dactylus on preserved material. De Man (1925) described the colour as being similar to *A. picteti* but more violet in parts. Juveniles and adults of *A. picteti* appear to differ so this species may also differ.

Distribution. Indonesia, S Sulawesi; Papua New Guinea, Central Province, Bougainville; shallow heights.

Remarks. De Man (1905) based *Axiopsis picteti* var. *spinimana* on two syntypes from the 'Anchorage off the south point of Kabaena-island', Indonesia (*Siboga* stn 209), the same locality at which he also recorded *A. picteti*. De Man (1925) described his two syntypes in moderate detail but illustrated only the distinctive cheliped.

Allaxiopsis bougainvillensis Sakai, 2011, is based on two female specimens (ZMB 14440) from Papua New Guinea, which Sakai referred to as the holotype with both chelipeds ('lectotype' in fig. 3 caption) and a paratype without chelipeds. They are correctly identified on the ZMB label as '*Axiopsis (Axiopsis) picteti* var. *spinimana* De Man, 1905', possibly by H. Schoede. In describing his new taxon, Sakai (2011) correctly stated that these specimens are not types but used this observation to justify a new species without stating how it differed from *A. (A.) picteti spinimana*. He did not illustrate or describe the distinctive spinose chelipeds of the holotype (photographs of which were provided to me by C.O. Coleman), which are clearly identical to those in De Man's (1925) figure of *A. spinimana* and to those figured here from other material. The supposed differences in gastric sculpture between *A. bougainvillensis* and *A. picteti* are small and not relevant.

The type locality of *A. bougainvillensis* was given by Sakai (2011) as 'Triop Bougainville, German New Guinea', a mistranscription of Tiop written on the label, which is now spelled Teop.

The species shares the trifold rostrum, regular pattern of blunt gastric spines, short scaphocerite, broad telson, uropodal endopod with shouldered anterior margin, and spinose uropodal rami with *A. picteti*. The most significant difference is the presence of chelipeds with spinose palms, the distal spines on the upper margin of the palm having a characteristic hooked form, characters that formed the basis of the identification of the Papua New Guinea specimens. Most of the characters of Sakai's (2011) diagnosis of this species are of generic value only.

Axiopsis Borradaile, 1903

Axiopsis pica Kensley, 2003

Figure 1d, e

Axiopsis pica Kensley, 2003: 363, figs 1, 2, pl. 1.—Ngoc-Ho, 2005: 51–55, fig. 2.

Axiopsis serratifrons.—Sakai, 2011: 56–63 (part).

Material examined. Papua New Guinea, Madang Province, PAPUA NIUGINI stations. Kranket I., outer slope, 05° 11.3' S, 145° 49.5' E, 1–24 m (stn PR129), IU-2013-7048 (female, 14.4 mm).

Mariana Islands. Guam Island, Apra Harbour, Middle Shoal, among coral rubble and rocks, 1 m, IU-2016-8007 (UF 2782), (1 ovigerous female, 16 mm); near Harbour entrance, among rocks, 8–12 m, IU-2016-8008 (UF 3021) (female, 13.5 mm).

Distribution. Guam (type locality), Papua New Guinea, French Polynesia; to 24 m depth.

Remarks. The single female from Papua New Guinea was first identified by its striking colour pattern, similar to that published

by Kensley (2003: pl. 1). Kensley (2003) noted that, as well as a distinctive colour, *Axiopsis pica* has 'a broader and more robust larger cheliped of pereopod 1 bearing flattened scale-like tubercles' than *A. serratifrons* with which it co-occurred. The upper margin of the propodus of the holotype and of the Papua New Guinea female is 1.5 times its greatest height. Kensley (2003) also compared his new species with material identified as *A. serratifrons* from Hawaii which has more slender chelipeds.

Ngoc-Ho (2005) compared specimens that she identified as *A. pica* from French Polynesia with a syntype of *A. serratifrons* also from Hawaii. The major cheliped of this syntype is twice as long as wide and smooth. Following Sakai's (2011) selection of the other syntype from Tonga as the lectotype (see below), comparison with Hawaiian specimens may be irrelevant.

Axiopsis pica co-occurs with *A. serratifrons* in both French Polynesia and Papua New Guinea. The major cheliped of the largest specimen is similarly proportioned, 1.5 times as long as wide, as of similarly-sized *A. serratifrons*. The most reliable morphological distinction between the two species can be found in the carapace. The carapace and pleon of *A. serratifrons* is smooth and flexible, with few scattered long setae, while that of *A. pica* is sclerotised, almost calcified and pitted with short stiff setae associated with the pits (Fig. 1d).

Axiopsis serratifrons (A. Milne-Edwards, 1873)

Figs 1f–i, 6a

Axia serratifrons A. Milne-Edwards, 1873: 263, pl. 13 figs 6, 6a.

Axiopsis serratifrons.—Snyder, 1923: 44, pl. 21 fig. 10.—Sakai and de Saint Laurent, 1989: 76.—Sakai, 2011: 56–63, fig. 9 (extended synonymy).

Material examined. Paralectotype. Hawaii, IU-2016-8115 (Th147) (male, 10 mm).

Papua New Guinea. Madang Province, PAPUA NIUGINI stations. Kranket I., outer slope, 05° 12.1' S, 145° 49.3' E, 17 m (stn PB02), IU-2013-302 (female, 9.3 mm); 05° 11.3' S, 145° 49.5' E, 1–11 m (stn PR225), IU-2013-7051 (male, 22 mm), NMV J71638 (ovigerous female, 22 mm); 05° 12' S, 145° 49' E, 10 m (stn PR99), IU-2013-7033 (ovigerous female, 9.5 mm). Rempi Area, S of Barag I., 05° 01.3' S, 145° 47.9' E, 2–13 m (stn PR61), IU-2013-638 (ovigerous female, 9.3 mm); S of lagoon inside bay, 05° 01.6' S, 145° 48.1' E, 2–15 m (stn PR69), IU-2013-7116 (male, 4.3 mm); outer slope, 05° 01.6' S, 145° 48.1' E (stn PR65), IU-2013-637 (male, 11.5 mm). Alexishafen, 05° 05.3' S, 145° 48.1' E, 1–6 m (stn PD31, IU-2013-7019 (male, 6.3 mm). W of Panab I., 05° 10.3' S, 145° 48.5' E, 1–18 m (stn PR147), IU-2013-7052 (female, 15.8 mm). Riwo waters, 3–15 m (stn PR109), IU-2013-7061 (male, 11.9 mm). S of Yabob I., 05° 15.5' S, 145° 47.3' E, 2–6 m (stn PD66), IU-2013-7098 (male, 5.8 mm). Ulimal I., 05° 05.6' S, 145° 48.7' E, 6 m (stn PS16), IU-2013-15308 (male, 10.0 mm).

New Ireland Province, Kavieng region, KAVIENG 2014 stations. Edmago I., 02° 36.9' S, 150° 44.4' E, 9 m (KZ2), IU-2014-826 (male, 8.6 mm); IU-2014-2685 (male, 9.3 mm). New Ireland mainland near N Cape, 02° 33.3' S, 150° 47.7' E, 1–20 m (stn KZ18), IU-2016-1011 (female, 12.5 mm). W side of Edmago I., 02° 37.1' S, 150° 44.2' E, 5–6 m (stn KZ20), NMV J71639 (ovigerous female, 10.5 mm). E side of Ral I., 02° 36.7' S, 150° 42.6' E, 3–10 m (stn KZ22), IU-2014-1090 (female, 10.6 mm). Byron Channel, SE Patio I., 02° 36.6' S, 150° 32.9' E, 2–7 m (stn KB40), IU-2014-2577 (ovigerous female, 10.9 mm). NE of Big Nusa I., entrance to Kavieng Harbour,

02° 33.7' S, 150° 49.1' E, 10 m (stn KZ11), IU-2014-2625 (ovigerous female, 10.6 mm). Mouth of Albatross Passage, E side, 02° 35.2' S, 150° 43.1' E, 13 m (KB72), IU-2016-8136 (juv., 5.0 mm). Between Big Nusa and Little Nusa Islands, 02° 34.6' S, 150° 46.3' E, 13–14 m (KB16), IU-2014-17688 (female, 6.9 mm). Eickstedt Passage W of Usien I., 02° 40.3' S, 150° 39.1' E, 9–11 m (KR70), IU-2014-17691 (male, 13.6 mm). Albatross Passage, 02° 44.6' S, 150° 42.8' E, 12–15 m (KD12), IU-2014-17692 (juv., 3.6 mm).

Colour. Variable. Generally reddish-orange, stronger colour on gastric carina; pleonal pleura with white patch anteroventrally; chelipeds similar or steel-blue, colour stronger at base of fingers (see figs 1f–i and Kensley [1981]).

Distribution. Widespread in the Indo West-Pacific, eastern Pacific (Hendrickx, 2008), south-west Atlantic (Sakai, 2011, 2015) and south-east Atlantic (Wirtz, 2009); subtidal.

Remarks. Of the two syntypic specimens from Samoa and Hawaii recorded by A. Milne-Edwards (1873), Sakai (2011) selected that from Samoa as the lectotype, not the one from Hawaii erroneously applied to the 'type locality' by Kensley (2003) and called 'holotype' by Ngoc-Ho (2005). This confusion was discussed by Komai and Tachikawa (2008). Sakai's (2011: figs 8A, B, 9) illustrations of the Samoan lectotype (ZMB K8405: checked for me by A. Brandt) are indistinguishable from Ngoc-Ho's (2005: fig. 3) of the Hawaiian paralectotype (MNHN IU-2016-8115 [Th147]). Sakai's (2011: fig. 8C) illustration of the Hawaiian paralectotype differs from both in appearing to have larger rostral teeth, the rostrum less evenly tapering, more teeth on the median carina (shown by my re-examination to have two on the rostrum, c. 15 on gastric region; fig. 6a), almost no spines on the lateral gastric carina (actually 13, 15), and fewer intermediate gastric tubercles (actually c. 20). The cheliped of the paralectotype lacks tuberculation on the propodal faces and the spine on the upper border of the merus, but these absences are common in juveniles of this size.

In an extensive synonymy, Sakai (2011) synonymised four species with *A. serratifrons*. The synonymy of *Axius affinis* De Man, 1888 (type locality, Ambon, Indonesia), *Axiopsis sculptimana* Ward, 1942 (type locality, Diego Garcia, Chagos Archipelago) and *Axiopsis brasiliensis* Coelho and Ramos-Porto, 1991, has not been disputed although a species with such a wide distribution suggests further examination is warranted as Komai and Tachikawa (2008) suspected. Kensley (1981) discussed the species in the Americas but his synonymy was limited. Ngoc-Ho (2005) recognised *A. pica* Kensley, 2003 (type locality, Guam), the fourth species synonymised by Sakai (2011), following a detailed justification and recorded it from French Polynesia. This synonymy is not recognised here (see *A. pica* above for discussion of differences).

Sakai's (2011) key to species of *Axiopsis* relied on the presence of a tooth on the upper margin of the merus and a smooth propodus of the cheliped to distinguish *A. consobrina* from *A. serratifrons* (without a tooth, with squamose propodus). Many smaller individuals, including ovigerous females, identifiable as *A. serratifrons* based on colour resemble *A. consobrina* De Man, 1905 in these features. De

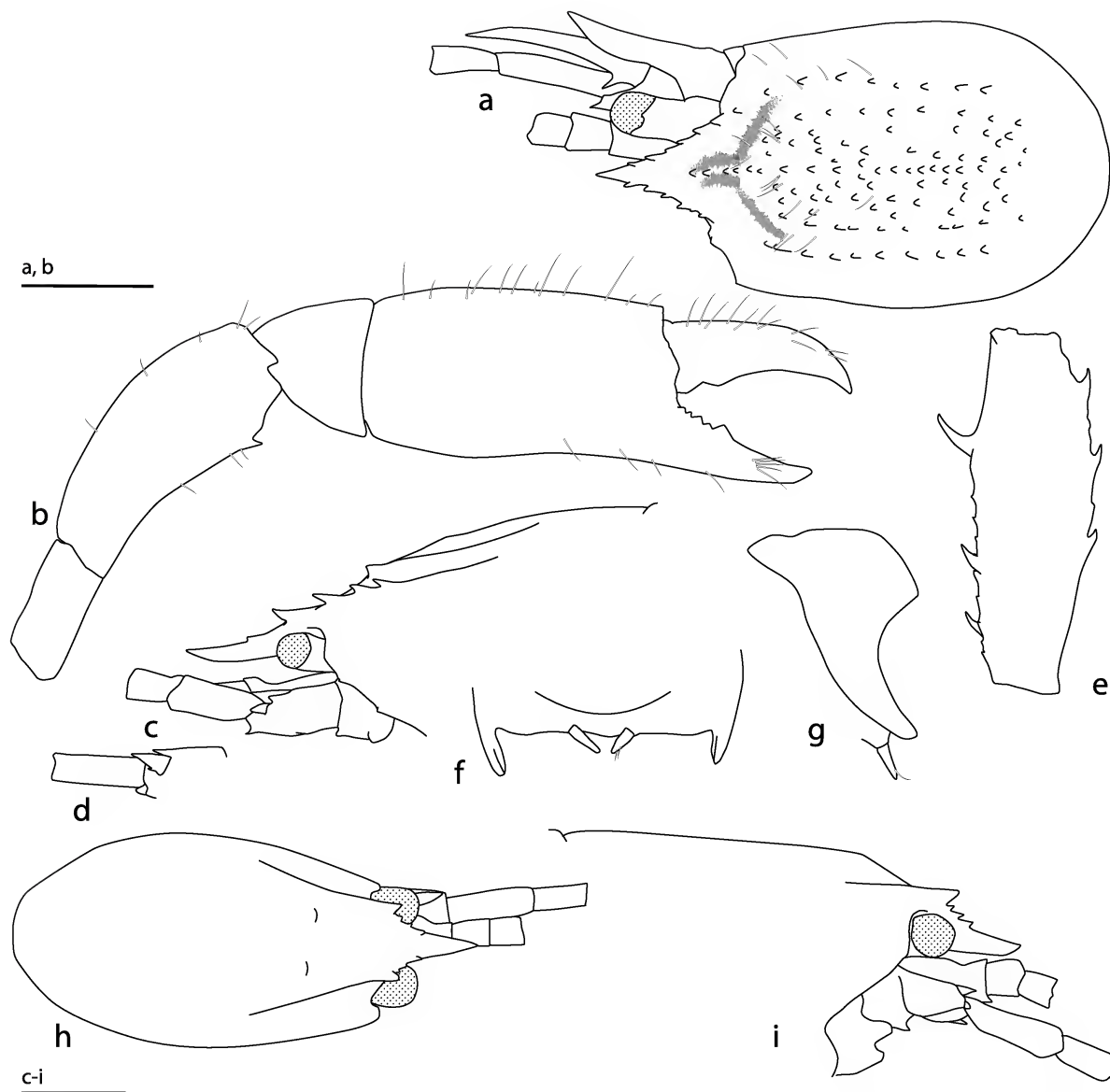


Figure 6. *Axiopsis serratifrons* A. Milne-Edwards, 1873: a, male, MNHN IU-2013-637, anterior carapace, dorsal view. *Parascytoleptus papua* Poore and Collins, 2010, male, MNHN IU-2013-7128: b, major right cheliped. *Paraxiopsis brocki* (De Man, 1888), male, MNHN IU-2013-7108: c, anterior carapace, lateral view; d, antenna with scaphocerite; e, cheliped, merus; male, MNHN IU-2014-2736; f, g, pleopods 1, ventral and lateral views. *Ralumcaris bisquamosa* (De Man, 1905), male, MNHN IU-2013-7120: h, i, anterior carapace, dorsal and lateral views. Scale bars = 1 mm.

Man (1905) distinguished *A. consobrina* on the absence of intermediate gastric teeth between the carinae and the palm of the smaller cheliped as long as the fingers but this is true only for the type. *Axiopsis consobrina* occurs usually from 75 m to a maximum of 310 m depth (Sakai, 2011; Vaitheeswaran, 2014) but Ngoc-Ho (2005) recorded one individual from 2.5 m depth. *Axiopsis serratifrons* is more immediately subtidal.

***Parascytoleptus* Sakai and de Saint Laurent, 1989**

***Parascytoleptus papua* Poore and Collins, 2010**

Figs 2a, b, 6b

Parascytoleptus papua Poore and Collins, 2010: 614–618, figs 1, 2.

Material examined. Papua New Guinea. Madang Province, PAPUA NIUGINI stations. N of Riwo mangrove and seagrass, 05°08.7'S,

145°48.2'E, 2 m (stn PB48), IU-2013-7100 (male, 2.6 mm). N of Sek I., inner slope, 05°04.7'S, 145°48.9'E, 3 m (stn PB50), NMV J71642 (2 males, 2.8, 3.1 mm).

New Ireland Province, Kavieng region, KAVIENG 2014 station. NW side of Ral I., coral wall, 19 m, 02° 36.4' S, 150° 42.4' E (stn KB62), IU-2014-2735 (female, 3.0 mm); IU-2014-17694 (male, 3.6 mm).

Distribution. Papua New Guinea, Madang and New Ireland provinces; 2–19 m depth.

Remarks. The types were collected not far from the new material. The major cheliped of the adult male figured here is longer and more elongate than that of the female figured by Poore and Collins (2010). Sakai (2011) diagnosed the genus with the male pleopod 1 'a small unsegmented protrusion' based on its presence on two males of 4.2 mm and 5.3 mm length. This has not been observed on the holotype of *P. papua* (4.2 mm) or the smaller males reported here. The pleopod 1 may appear only in larger specimens.

Paraxiopsis De Man, 1905

Remarks. Two of the 16 known species were found in Papua New Guinea and are diagnosed here with a minimal character suite.

Paraxiopsis austrinus (Sakai, 1994)

Eutrichocheles austrinus Sakai, 1994: 185, figs. 6, 7.—Sakai 2011: 111.

Paraxiopsis austrinus.—Kensley 2003, 373.—Poore and Collins 2009: 266, fig. 29.

Material examined. Papua New Guinea. New Ireland Province, Kavieng region, KAVIENG 2014 stations. Mouth of Albatross Passage, E side, 02° 35.2' S, 150° 43.1' E, 13 m (stn KB72), IU-2014-1046 (male, 6.1 mm). S coast of Baudison I., 02° 45.2' S, 150° 41.7' E, 22–27 m (stn KB68), IU-2014-1153 (male, 7.6 mm; ovigerous female, 6.3 mm). E of Albatross Passage, 02° 45.2' S, 150° 43.4' E, 13–17 m (stn KB24), IU-2014-2364 (male, 9.0 mm).

Diagnosis. Carapace smooth, with tomentum of short and longer setae. Rostrum with 0–3 small lateral teeth; lateral gastric carina with supraorbital spine plus 2 teeth; submedian gastric carina with 6–8 teeth; median gastric carina without spines. Telson with 3 or 4 pairs of dorsal spines. Cheliped merus with 2 spines on upper margin, palm unornamented. Male pleopod 1 absent in small specimens, single article in adults.

Distribution. Northern Australia; New Ireland Province, Papua New Guinea; to 27 m depth.

Remarks. The new material extends the range of this species from Darwin, northern Australia, to Papua New Guinea. The species differs from the original description only in having no rostral spines (three small spines in Australian specimens) and in having one (rather than two) post-supraocular spine on the lateral gastric carina. All of the males lack pleopod 1 but possess a minute tubercle in its place. Kensley (2003) and Poore and Collins (2009) justified the generic placement of this species.

Paraxiopsis brocki (De Man, 1888)

Figs 2c, d, 6c–g

Axius brocki De Man, 1888: 475, pl. 20 fig. 3.

Axiopsis (*Paraxiopsis*) *brocki*.—De Man, 1905: 597.—Tirmizi, 1983: 88–90, fig. 3.

Eutrichocheles brocki.—Sakai and de Saint Laurent, 1989: 52, fig. 4B.—Ngoc-Ho, 1998: 365–368, fig. 1.

Paraxiopsis brocki.—Kensley, 1996.—Poore and Collins, 2009: 266.—Sakai, 2011: 158–161, fig. 27C (full synonymy).

Material examined. Papua New Guinea. Madang Province, PAPUA NIUGINI stations. W of Panab I., 05° 10.3' S, 145° 48.5' E, 1–18 m (stn PR147), IU-2013-7108 (male, 6.8 mm). Riwo, mangrove, 05° 09' S, 145° 48.2' E, 1–2 m (stn PR235), IU-2013-7118 (ovigerous female, 5.5 mm). Kranket I., Cape Jantzen, 05° 12.5' S, 145° 49.1' E, 13 m (stn PB11), IU-2013-7126 (male, 3.1 mm).

New Ireland Province, Kavieng region, KAVIENG 2014 stations. S coast of Baudison I., 02° 45.2' S, 150° 41.7' E, 22–27 m (stn KB68), IU-2014-990 (female, 5.5 mm); IU-2014-1032 (female, 5.9 mm). NW point of Nusa I., 02° 33.9' S, 150° 46.7' E, 15–17 m (stn KB04), IU-2014-2054 (juvenile, 3.1 mm). Marthas Shoal, sand and coarse rubble in gutter, 20 m, 02° 32.5' S, 150° 35.3' E (stn KB60), NMV J71640 (male, 7.5 mm; 2 ovigerous females, 6.8 mm); IU-2014-2736 (male, 6.8 mm). NW point of Nubis I., 02° 37.2' S, 150° 31.8' E, 20 m (stn KB39), IU-2014-17693 (juvenile, damaged).

Indonesia. Maluku Province, Pulau Wuliaru, 7° 27' S, 131° 3.7' E, IU-2014-12081 (female, 9.5 mm).

Diagnosis. Carapace smooth, without tomentum of setae. Rostrum with 4–6 lateral teeth; lateral gastric carina with supraorbital spine plus 2 teeth; submedian gastric carina with 1 or 2 teeth; median gastric carina without spines. Telson with 3 or 4 pairs of dorsal spines. Cheliped merus with 1–3 spines on upper margin, palm unornamented. Male pleopod 1 absent in small specimens, single article in adults.

Distribution. Widespread in the Indo West-Pacific, from eastern Africa, Western Australia, northern Australia, to southern Japan and French Polynesia; to 91 m depth (Sakai, 2011).

Remarks. The new material contributes little to knowledge of this widespread and frequently taken species. The species was well illustrated by Ngoc-Ho (1998). Sakai (2011: fig. 27C) figured a simple male pleopod 1 on a male from Darwin, Australia; pleopod 1 is absent in the smallest male and minute in the larger ones from this collection. Most of the specimens at hand have a minute anterior tooth on pleonal pleura 2–5. Sakai (2011) himself discussed variation in this character and in the presence or absence of the male pleopod 1 after presenting an extensive diagnosis.

Ralumcaris Sakai, 2011

Ralumcaris Sakai, 2011: 182–183.

Ralumcaris bisquamosa (De Man, 1905)

Figs 2e, 6h, i

Axiopsis (*Paraxiopsis*) *bisquamosa* De Man, 1905: 597.—De Man, 1925: 7, 72, 109, pl. 8 fig. 20–20c, pl. 9 fig. 20d–m.—Holthuis, 1953: 51.

Eutrichocheles bisquamosa.—Sakai and de Saint Laurent, 1989: 53, fig. 15.—Kensley, 1994: 822.

Paraxiopsis bisquamosa.—Kensley, 1996: 711, 712.—Kensley, 2003: 372, table 2.

Ralumcaris bisquamosa.—Sakai, 2011: 183–185, figs 33, 34.

Material examined. Papua New Guinea. Madang Province, PAPUA NIUGINI stations. Rempi Area, W of Barag I., 05° 01.2' S, 145° 47.9' E, 5–10 m (stn PD45), IU-2013-7130 (male, 2.6 mm). N of Kranket I., 05° 11.3' S, 145° 49.6' E, 5 m (stn PB47), IU-2013-7037 (ovigerous female, 3.6 mm). Cape Barschtch, 05° 03.9' S, 145° 48.8' E, 12 m (stn PB27), IU-2013-7119 (male, 3.2 mm). Tab I., inner slope, 05° 10.1' S, 145° 50.2' E, 1–4 m (stn PR162), IU-2013-7120 (male, 4.1 mm).

New Ireland Province, Kavieng region, KAVIENG 2014 stations. Steffen Strait, W side of Wade I., 02° 39.5' S, 150° 37.7' E, 15 m (stn KS31), IU-2014-2451 (juvenile damaged), IU-2016-8135 (juvenile, 2.9 mm). W side of Tsoilaunung I., 02° 32.8' S, 150° 30.8' E, 6 m (stn KB48), IU-2014-2619 (ovigerous female, 5.9 mm). Tab I., N.L. Bruce, 05° 10' S, 145° 51' E, NMV J34090 (ovigerous female, 4.2 mm).

Distribution. Indonesia, Papua New Guinea, Mariana Is; 1–36 m depth.

Remarks. Kensley (1996) pointed out the differences between *Paraxiopsis bisquamosa* and the remaining species of this genus and excluded the species from *Paraxiopsis* as redefined by him. Sakai (2011) described and figured De Man's holotype (ZMA Crust. De. 102.674) but labelled it as 'lectotype'.

Micheleidae Sakai, 1992

Michelea Kensley & Heard, 1991

Michelea papua sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:37FAF4C1-2B8E-44AA-B357-783EDE48B9FD>

Figure 7

Material examined. Holotype. Papua New Guinea. New Ireland Province, N of Kobotteron I., 02° 36.4' S, 150° 42.4' E, 2–3 m, reef wall and rubble, (KAVIENG 2014 stn KB62), IU-2013-2781 (male, 3.2 mm).

Diagnosis. Gills fully developed. Pleopods 2, 3, 5 with 18/6, 18/8 and 25/13 marginal lamellae on endopods/exopods, respectively (pleopod 4 unknown). Telson tapering to rounded apex, length 1.15 width. Maxilliped 3 ischium with obsolete crista dentata; merus with mesial tooth.

Description. Cephalothorax 0.4 total length, about 1.65 times as long as greatest height; rostrum triangular, about half as long as basal width, slightly depressed distally, about 0.4 as long as eyestalks; cervical groove weakly defined, reaching 0.6 length of cephalothorax; longitudinal setal-row level with lateral margin of eyestalk, of 5 setae; vertical setal-row of 5 setae below horizontal row and 2 setae near cervical groove.

Pleomere 1 with dorsolateral longitudinal setal-row of 10 setae. Pleomeres 2–6 each with transverse setal-rows of 6–7 setae near midpoint; all somites also with groups of long simple setae, none with marginal setal-rows.

Antennule with elongate waisted article 1, 0.6 length of cephalothorax; articles 2 and 3 subequal, each about 0.25 length of article 1; flagella with 11 and 9 articles, longer than peduncle. Antenna with distinct articulating scaphocerite,

about half length of article 2; article 4 reaching to middle of article 3 of antennule; article 5 short; flagellum missing.

Mandible, maxillules, maxillae, maxillipeds 1 and 2 typical of genus. Maxilliped 3 ischium with obsolete crista dentata; merus with strong mesial tooth on right of pair only (absent on left); exopod 1.6 times ischium length.

Chelipeds equal; ischium with weak lower tooth; merus with weak tooth on slightly convex lower margin, upper margin more convex proximally than distally, 1.8 times as long as high; carpus unarmed; propodus almost cylindrical, 3.6 times as long as high; fixed finger 0.35 total length of propodus, its cutting edge with long obsoletely bicuspid tooth at midpoint; dactylus cutting edge straight, curved distally, equal to fixed finger.

Pereopod 2 unknown. Pereopod 3 propodus 2.5 times as long as wide, with 2 spiniform setae on distal-upper mesial face, 6 on distal-lower face; and 2 transverse setal-rows of 1 and 2 setae; dactylus with 2 spiniform setae on upper margin. Pereopod 4 propodus 3.8 times as long as wide, with 7 spiniform setae on upper margin, 5 on lower margin; with 2 transverse setal-rows each of 2 setae; dactylus with 5 spiniform setae on upper-mesial margin. Pereopod 5 subchelate; fixed finger with 4 distal spiniform setae; dactylus without spiniform setae.

Pleopod 1 of male lobed mesially, expanded distally, with c. 8 minute hooks, setose around midpoint and laterally, and with 5 simple seta laterally. Pleopod 2 with appendix interna sac-like, 2.5 times as long as wide; appendix masculina narrow, about third long as endopod; with 18 lamellae on lateral margin of endopod, 6 on distolateral margin of exopod. Pleopod 3 with 18 lamellae on lateral and distomesial margin of endopod, 8 on lateral margin of exopod; pleopod 4 unknown; pleopod 5 with 25 lamellae on endopod, 13 on exopod.

Telson tapering to rounded apex from one-third length; 1.15 times as long as wide. Uropodal endopod ovate, 1.5 times as long as wide, anterior margin straight, distal margin semicircular, without distal tooth, posterior margin convex; exopod ovate, 1.7 times as long as wide, anterodistal margin with 16 short spiniform setae, posterior margin with 6 blade-like setae.

Branchial formula as in *M. kalbarri* Poore and Collins, 2015.

Distribution. Papua New Guinea. New Ireland Province (03° S, 151° E), 2–3 m. depth (known only from type locality).

Etymology. From Papua New Guinea; noun in apposition.

Remarks. *Michelea papua* resembles *M. imperieusae* Poore and Collins, 2015, from north-western Australia in having similar numbers of pleopodal lamellae but differs in the short broad rostrum (not spine like), longer antennae, and more elongate maxilliped 3 and pereopodal articles.

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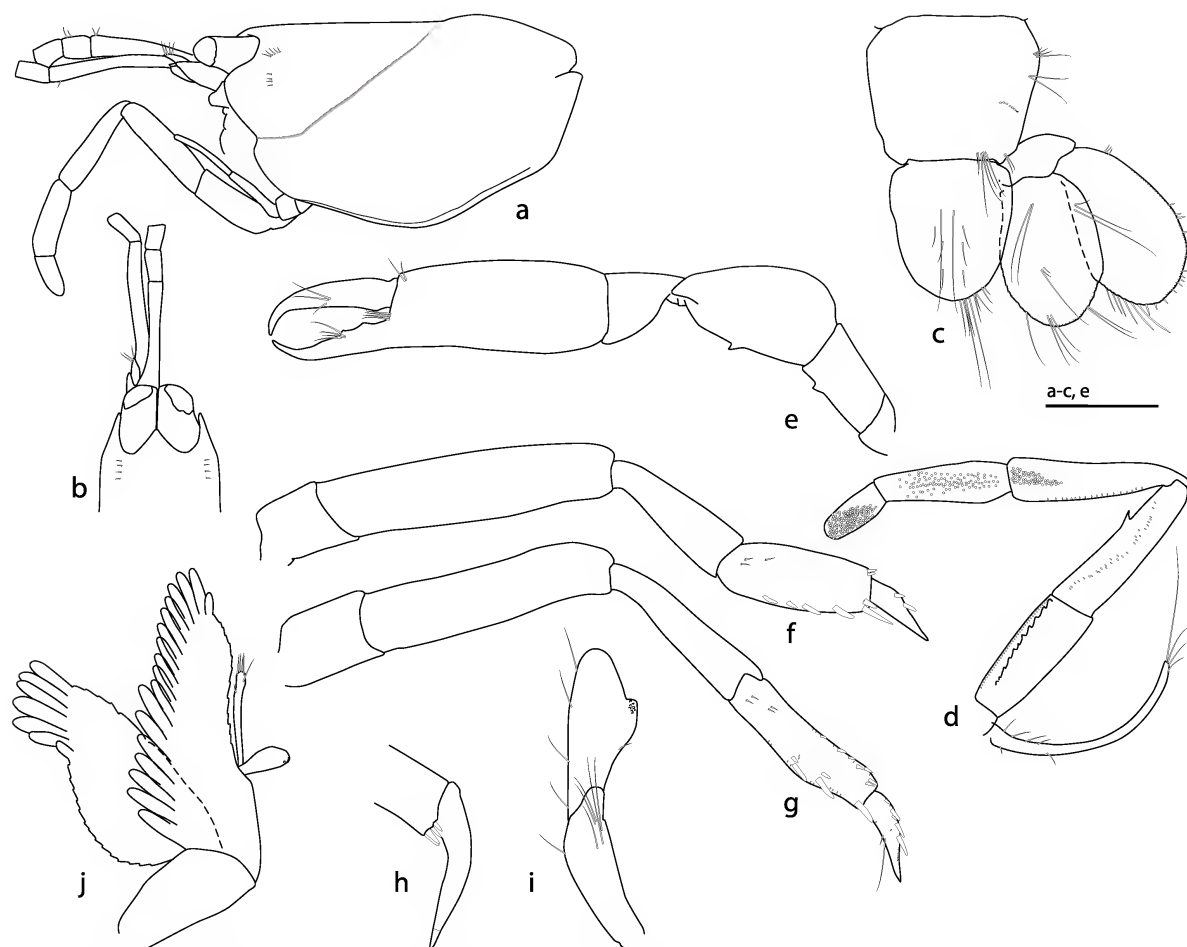


Figure 7. *Michelea papua* sp. nov., holotype: a, lateral carapace, antenna, antennule, maxilliped 3; b, carapace, antenna, antennule; c, pleomere 6, telson, uropod; d, maxilliped 3; e, f, g, pereopods 1, 3, 4; h, pereopod 5 dactylus; i, j, pleopods 1, 2. Scale bar = 1 mm.

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The Indo-West Pacific species of *Neaxiopsis* and *Neaxius* (Crustacea: Axiidea: Strahlaxiidae)

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Abstract

Poore, G.C.B., and Dworschak, P.C. (2018). The Indo-West Pacific species of *Neaxiopsis* and *Neaxius* (Crustacea: Axiidea: Strahlaxiidae). *Memoirs of Museum Victoria* 77: 15–28.

The synonymy of *Axius* (*Neaxius*) *gundlachi* var. *orientalis* De Man, 1925, with *Axius* (*Neaxius*?) *euryrhynchus* De Man, 1905, now *Neaxiopsis euryrhynchus* (De Man, 1905), is confirmed. The synonymy of *Axia acantha* (A. Milne Edwards, 1879), *Eiconaxius taliliensis* Borradaile, 1900, and *Axius acanthus mauritanus* Bouvier, 1914, is confirmed; they are a single species, *Neaxius acanthus*. They and a second species from the Indo-West Pacific, *Neaxius trondlei* Ngoc-Ho, 2005, are not synonyms of *Neaxius glyptocercus* (von Martens, 1868), as was proposed in Sakai's (2011) family synthesis. Instead, a second species (from southern Queensland, Australia, Fiji and French Polynesia) close to *Neaxius glyptocercus* from north-eastern Australia is diagnosed as *Neaxius capricornicus* sp. nov.

Keywords

Crustacea, Strahlaxiidae, *Neaxiopsis*, *Neaxius*, taxonomy

Introduction

Attempts to identify specimens of Strahlaxiidae, one from the western Indian Ocean and others from throughout the Indo-West Pacific, led us into a web of confused names and errors in the most recent catalogue and review of the family (Sakai, 2011). Here, this confusion is resolved after examination of a wide range of material from across the Indo-West Pacific.

We test the assumption that *N. acanthus* (A. Milne Edwards, 1879) is widespread by reviewing collections from a wide geographic range, and re-diagnose the three known Indo-West Pacific species: *N. acanthus*, *N. glyptocercus* (von Martens, 1868) and *N. trondlei* Ngoc-Ho, 2005. In the process, a fourth undescribed species is uncovered.

Species are differentiated, in part, by the number of spines along certain margins. These can vary between individuals, and between left and right sides. Here, for each character we provide median numbers of spines followed by a range or outlying value in parentheses.

The bulk of the material is lodged in the Muséum nationale d'Histoire naturelle, Paris (MNHN) (IU-prefixes; former registration numbers with Th prefix). Others are from the collections of the Australian Museum, Sydney (AM); Museums Victoria, Melbourne (NMV); Naturhistorisches Museum, Vienna (NHMW);

National Museum of the Philippines, Manila (NMCR); University Museum of Zoology, Cambridge (UMZC); Zoologisches Museum, Berlin (ZMB); Zoological Museum, Hamburg (ZMH); and the Zoological Reference Collection, Lee Kong Chian Natural History Museum (previously known as Raffles Museum of Biodiversity Research), National University of Singapore (ZRC). Size of specimens is given as carapace length (cl) unless otherwise stated (total length, tl).

Strahlaxiidae Poore, 1994

Strahlaxiidae Poore, 1994: 100.—Sakai, 2011: 319–320.

Remarks. The diagnosis of the family stands. It was elaborated by Sakai (2011) without providing any more diagnostic characters. Poore (1994) and Sakai (2011) both provided keys to the three genera.

Neaxiopsis Sakai and de Saint Laurent, 1989

Neaxiopsis Sakai and de Saint Laurent, 1989: 32.—Poore, 1994: 100.—Sakai, 2011: 320.

Remarks. The genus is recognisable from the broad plate-like rostrum with an apical notch. Sakai (2011) provided a key to distinguish the two species but confused their synonymies.

***Neaxiopsis euryrhynchus* (De Man, 1905)**

Axius (*Neaxius*?) *euryrhynchus* De Man, 1905: 590.—De Man, 1925c: 3, 12, 31, pl. 1 fig. 2.

Axius (*Neaxius*) *gundlachi* var. *orientalis* De Man, 1925b: 122–125, fig. 2, 2b.—De Man, 1925c: 4, 12, 31 (type locality: Matupi [now Matupit I.] near Rabaul, New Britain, Papua New Guinea).

Axius (*Neaxius*) *euryrhynchus*.—Miyake, 1982: 90, 192 (list), pl. 30 fig. 5.

Neaxiopsis euryrhynchus.—Sakai and de Saint Laurent, 1989: 33.

Neaxiopsis euryrhyncha.—Sakai, 2011: 321–323, fig. 60.

Material examined. Réunion. Off Sainte Anne, 21° 00.6' S, 55° 43.8' E, 45 m (Expedition MD32 stn DR154), MNHN IU-2016-8079 (male, 3.5 mm).

Type locality. Anchorage off Dongala, Palos-bay, Sulawesi, Indonesia, 36 m (*Siboga* stn 86).

Distribution. Japan; Indonesia, Sulawesi; Papua New Guinea, New Britain; Réunion; to 36 m depth.

Remarks. De Man (1925c) believed that the syntypes of *Axius* (*Neaxius*?) *euryrhynchus* are “a very young stage” of *Axius* (*Neaxius*) *gundlachi orientalis*, both described by him from the south-western Pacific. He synonymised the two names. Sakai (2011) argued first (p. 321) that *Neaxiopsis euryrhynchus* and *N. gundlachi* von Martens, 1872, a species from the Caribbean, are distinct species but then argued (pp. 323–324) for the synonymy of “*N. orientalis*” and *N. gundlachi*. He said both share a row of tubercles along the carina of the pereopod 1 palm but did not explain the state of this character in *N. euryrhynchus*. On purely biogeographic criteria, De Man’s synonymy is the more probable.

Miyake (1982) recorded a female with total length of 69 mm from Japan. Sakai and de Saint Laurent (1989) doubted this was the same species on the basis of its size. The syntypes of *A. (N.?) euryrhynchus* are 11 mm long juveniles, while the syntypes of *A. (N.) gundlachi orientalis* range in length from 48 to 74 mm. Miyake’s (1982) specimen is within this range.

The specimen from Réunion is very small but shares the characteristic rostrum, cheliped dentition and tail fan. Assuming cryptic species are not involved, the record extends the species’ range throughout the Indo West-Pacific.

The specific name is a noun and does not follow the gender of the genus name.

***Neaxius* Borradaile, 1903**

Axius (*Neaxius*) Borradaile, 1903: 537.—De Man, 1925c: 12.

Neaxius.—Sakai and de Saint Laurent, 1989: 29.—Poore, 1994: 100.—Sakai, 1994: 176.—Sakai, 2011: 324–325.

Type species. *Axia acantha* A. Milne-Edwards, 1879, by original designation.

Remarks. Specimens of the type species, now *N. acanthus* (A. Milne-Edwards, 1879) from the type locality, New Caledonia, have never been illustrated, and Milne-Edwards’ (1879) description is too general to be certain of the species’ identity: he described the antenna as having four or five lateral spines, the anterior carapace margin with four or five spines, the cervical groove with three or four spines, and the scaphocerite with one mesial and four lower spines. This description applies to many

specimens throughout the Indo West-Pacific and the species has been assumed to be widespread. The standard reference for details of this species is De Man’s (1898) description and illustrations of specimens from Sulawesi, Indonesia, not those from the type locality. Sakai and de Saint Laurent (1989) were the first to include type material in their appraisal of *N. acanthus*.

Borradaile (1903) synonymised without comment *Eiconaxius taliliensis* Borradaile, 1900, with *N. acanthus*. *Axius acanthus* var. *mauritanica* Bouvier, 1914, has also long been thought to be a junior synonym. This synonymy was accepted by Ngoc-Ho (2006) who tabulated differences between the six accepted species of *Neaxius*, three from the Indo-West Pacific and three from the Atlantic Ocean.

Sakai (2011: 329–330, figs 61, 62) took a different view and treated all nominal Indo-West Pacific species and subspecies – *Axia acantha* (type locality: New Caledonia), *Eiconaxius taliliensis* (New Britain), *Neaxius trondlei* Ngoc-Ho, 2005 (Marquesas Islands) and *Axius acanthus* var. *mauritanicus* (Mauritius) – as synonyms of *Axius glyptocercus* von Martens, 1868 (Cape York, Qld, Australia), which he believed to be a variable species. He described and figured the antenna, carapace spination and scaphocerite of specimens from Fiji, Tahiti, Palau, Sulawesi and Ryuku, Japan, to justify that only one species, *Neaxius glyptocercus*, was distributed widely in the Indo-West Pacific. He argued that the variability in a population of *N. acanthus* from Motupore, Papua New Guinea, studied by Mukai and Sakai (1992) (5–7 spines on the cervical groove, 1 or 2 mesial and 3–6 lateral spines on the second antenna article, spinose merus on pereopod 2) supports his view, but in reality, they confirm the opposite. This population differs consistently from *N. glyptocercus* in having the cervical groove, antenna article and pereopod 2 unarmed as in all Australian specimens examined by Poore and Griffin (1979) and in more recently examined examples (AM, NMV, NHMW, ZMH). To these characters can be added differences in the shape and ornamentation of the telson. The telson of *N. glyptocercus* is c. 1.3 times as wide as long, moderately tapering, with 1 or 2 small spines along the lateral margin, with the anterior transverse ridge reaching the lateral margins, and the posterior concave face without ornamentation. The telson of *N. acanthus* is 1.5 times as wide as long, strongly tapering, with 1–6 tubercles above each posterolateral margin, with the second transverse ridge one-third of the way between the first and the posterior margin, and with a third short obsolete transverse ridge and longitudinal lateral buttresses emerging from the ends of the second transverse ridge.

This separation is, however, confused by the discovery that southern and Pacific representatives of “*N. glyptocercus*” are morphologically distinct and warrant description of another species, *Neaxius capricornicus* sp. nov. This confusion has led to errors in the identification of species for which sequences are registered in Genbank at the National Center for Biotechnology Information (<https://www.ncbi.nlm.nih.gov/nuccore/neaxius>) (Table 1).

Tsang et al. (2008) showed on the basis of three rRNA sequences that *N. acanthus* from Taiwan differs from *N. capricornicus* from Australia (wrongly identified as *N. glyptocercus*) with 100% probability.

Table 1. Present identifications of species of *Neaxius* recorded in Genbank (National Center for Biotechnology Information)

Accession no.	Sequences	Citation	Locality/voucher number	Identification
EF585463.1 EF585474.1 EF585452.1	18S, 28S, 16S subunits ribosomal RNA	Tsang et al., 2008 (as <i>N. acanthus</i>)	Taiwan/NTOU A00421	<i>N. acanthus</i>
NC_019609 JN897379.1	mitochondrion, complete genome	Lin et al., 2012 (as <i>N. glyptocercus</i>) Kensley et al., 2000 (as <i>N. acanthus</i>)	Kenting, Taiwan/NTOU	<i>N. acanthus</i>
KC107821.1	mitochondrion, partial genome	Shen et al., 2013 (as <i>N. acanthus</i>)	Indonesia, Sulawesi/ no voucher	<i>N. acanthus</i>
EU874994.1 EU874944.1	18S, 16S subunits ribosomal RNA	Tudge and Cunningham, 2002; Tsang et al., 2008; Robles et al., 2009 (as <i>N. glyptocercus</i>)	Australia, S Qld/ NMV J39643	<i>N. capricornicus</i>

Anker et al. (2015) illustrated in colour specimens of what are clearly *N. acanthus* from Lombok, Indonesia, as *N. glyptocercus*, but expressed confusion over Sakai's synonymy. Sakai (2017) repeated his incorrect diagnosis of "*N. glyptocercus*" and figured a cheliped from Japan clearly of the *N. acanthus* form.

The four Indo-West Pacific species of *Neaxius* are here diagnosed with the same character suite. Major diagnostic characters of *N. acanthus*, *N. capricornicus* sp. nov. and *N. glyptocercus* are compared in fig. 8. The distributions of all species in the Indo-West Pacific are shown in fig. 9.

Neaxius acanthus (A. Milne Edwards, 1879)

Figures 1–5, 8a–f

Axia acantha A. Milne-Edwards, 1879: 110.

Eiconaxius acanthus.—De Man, 1896: 491–497.—De Man, 1898: 700, pl. 34 fig. 57 (West-Celebes = Indonesia, Sulawesi).

Eiconaxius taliliensis Borradaile, 1900: 420–421, fig. 15a–c.

Axius acanthus.—Borradaile, 1903: 537 (listed as type species of *Neaxius*).

Axius taliliensis.—Borradaile, 1903: 537 (as synonym of *Axius (Neaxius) acanthus* A. Milne-Edwards, 1879).

Axius acanthus var. *mauritiana* Bouvier, 1914: 704.

Axius (Neaxius) acanthus var. *mauritanus*.—Bouvier, 1915: 196–198, fig. 7.—Fourmanoir, 1955 31, fig. 4.—De Man, 1925c: 3, 10, 14.

Axius (Neaxius) acanthus.—De Man, 1925a: 50–55.—De Man, 1925c: 3, 14 (part).—Poore and Griffin, 1979: 235–236, fig. 7 (Qld, Australia).—Tirmizi, 1983: 85–88, figs 1, 2 (Maluku, Indonesia).—Holthuis, 1953: 51 (Marianas Is, Saipan).—Miyake, 1982: 93 (Japan).—Sakai, 1987: 303, 304 (Japan).

Neaxius acanthus.—Sakai and de Saint Laurent, 1989: 30–31.—Mukai and Sakai, 1992: 47–52, fig. 1 (Papua New Guinea).—Sakai, 1994: 200.—Kensley et al., 2000: 212, figs 5, 7F (Taiwan).—Kensley, 2003: 383 (Guam).—Kneer, 2006; Kneer, Asmus, Ahnelt and Vonk, 2008; Kneer, Asmus and Vonk, 2008 (Bone Batang I., S Sulawesi, Indonesia).—Sakai and Sawada, 2006: 1357 (Japan).—Tsang et al., 2008: 218–219 (Taiwan).—Tan et al., 2017: 5 (comment on name).

Neaxius glyptocercus.—Sakai, 2011: 326–331 (part) figs 61B, 62C, D (not figs 61A, C–E, 62A, B, E, F [interchanged with 61B]), = *N. glyptocercus* (von Martens, 1868.—Lin et al., 2012: 2–9 (Taiwan, misidentification).—Anker et al., 2015: 335, figs 25, 26.—Sakai, 2017: 188, fig. 3A.

Type material examined. Lectotype of *Axia acantha*. New Caledonia. MNHN IU-2014-11315 (Th812) (female, tl 72 mm, dry). Paralectotype, MNHN IU-2014-11316 (Th190) (male, cl 27 mm) (Fig. 1).

Syntypes of *Axius acanthus mauritiana*. Mauritius. Le Chaland, MNHN IU-2014-11317 (Th191), ovigerous female, tl 69 mm (Bouvier, 1915, listed 2 specimens from this locality). Port Louis, MNHN IU-2014-11318 (Th192), 1 male, tl 58 mm; 2 ovigerous females, tl 67, 62 mm (as listed by Bouvier, 1915) (Fig. 2).

Syntypes of *Eiconaxius taliliensis*. Papua New Guinea, New Britain, Talili Bay, UMZC I.57590 (male, 22.3 mm; ovigerous female, 19.4 mm) (Fig. 3).

Other material examined. Specimens marked * were listed by Sakai and de Saint Laurent (1989).

Tanzania. Mombasa, Levin Reef, MNHN IU-2016-8073 (Th780*) (1 individual).

Madagascar. Nosy Iranja, IU-2014-22792 (Th454*) (1 individual). Nosy Bé, IU-2014-22793 (Th456*) (2 individuals); IU-2016-8071 (Th455*) (3 individuals); NHMW 19385 (male, 26.3 mm, broken); NHMW 19386 (1 male, 24.5 mm, telson damaged); NHMW 19387 (fragments of 2 specimens); NHMW 24999 (female, 23.7 mm + exuvia). Nosy Bé, Palm Beach Hotel Bay, sand between coral rubble, 3 m. Sainte Luce, W of Ilot Babet, 24° 46.2' S, 47° 12.4' E, 1–10 m (ATIMO VATAE stn TA63) IU-2010-4331 (1 damaged individual).

Glorieuse Is, Grande Glorieuse I., IU-2016-8072 (Th451*) (1 individual).

Mayotte. IU-2014-22789 (Th1565) (1 individual); IU-2014-22790 (Th1564) (1 individual).

Indonesia. Sulawesi, Bone Batang I., NHMW 25859 (male, 10.3 mm). Bali, Nusa Dua, intertidal seagrass, NHMW 25854–25858 (male 15.3 mm; 4 juveniles, 7.1–11.1 mm).

Papua New Guinea. Central Province, Motupore I., 09° 32' S, 147° 17' E, NMV J17235 (3 males, 21.9–27.5 mm; 2 ovigerous females, 20.3, 27.5 mm). Madang Province, Jais Aben Resort, Riwo, seagrass,

05° 09' S, 145° 48.2' E, 1–3 m (PAPUA NIUGINI stn PR195-A), MNHN not registered (photo only seen).

Malaysia. Sipadan, IU-2016-8070 (1 individual).

Palau. ZMH K8411 (female, 17.1 mm).

Philippines. Bohol, Panglao I., Balicasag I., NMCR 39107 (25.8 mm); NHMW 25860 (male, 25.7 mm); ZRC 2017.0415 (male, 15.5 mm); ZRC 2017.0416 (male, 17.4 mm); MNHN-2016-3495 (male, 20 mm); NMCR 39108 (female, 20.6 mm). Momo Beach, 9° 36.1' N, 123° 45.2' E, NHMW 25861 (male, 20 mm); NHMW 25862 (male, 25.8 mm). Looc, sand and seagrass with coral patches, 9° 35.7' N, 123° 44.4' E, 4 m, NHMW 25863 (male, 19.5 mm).

Taiwan, Pingtung County, Banna Bay, 10 m, NHMW 25919 (male, 10.4 mm), NHMW 25923 (juvenile, 7.1 mm).

Japan. Ryuku Is., Ishigakaki I., IU-2016-8078 (Th865*) (9 individuals); IU-2016-8075 – 8077 (3 dry individuals).

New Caledonia. IU-2016-8080 (Th511*) (13 individuals). Bourail, IU-2016-8074 (Th1488) (1 individual). Ouano Plage, IU-2014-22791 (Th1486) (1 individual).

Diagnosis. Carapace supra-antennal margin without anteriorly directed spine; anterolateral margin with 6 (4, 5) prominent spines, dorsalmost anteriorly directed; branchiostegite anterior margin unarmed; cervical groove with 4 (0–7) sharp spines along posterior margin. Telson 1.3–1.5 times as wide as long; tapering strongly from widest point to posterior margin, posterior margin about half greatest width; anterior transverse ridge straight, curving laterally but not reaching lateral margin at its widest point; posterior transverse ridge situated at 0.35–0.4 distance between anterior ridge and posterior margin; posterolateral margin with 2–6 obsolete submarginal tubercles; posterior face concave, with obsolete third transverse ridge, with pair of sublateral longitudinal ridges subtended from ends of second transverse ridge, each with 2 (1–3) rounded tubercles, sometimes obsolete. Antenna article 2 with 1 (2) upper-mesial spine, 3 (0–6) lateral spines; scaphocerite with 1 (2) mesial sharp spine, 5 (2–6) sharp ventral spines;



Figure 1. *Axia acantha* A. Milne-Edwards, 1879, lectotype, MNHN IU-2014-11315: a, dorsal view; b, lateral left view; c, lateral right view; d, telson and uropods. Paralectotype, MNHN IU-2014-11316: e, dorsal view; f, lateral left view; g, telson and uropods.

article 4 lower margin with 3 (0–5) sharp spines. Cheliped merus, lower margin with 4 (2–5) spines, lateral face with curved row of 8 (5–10) spines. Pereopod 2 merus, lower margin with row of 10 (8–17) spines. Pereopod 3 merus, lower margin without row of spines.

Remarks. A. Milne-Edwards (1879) did not specify how many specimens he had. Two remain in MNHN, one of which Sakai and de Saint Laurent (1989) called the type. This was an effective lectotype designation. This and many more from New Caledonia were examined.



Figure 2. *Axius acanthus mauritiana* Bouvier, 1914, syntype, MNHN IU-2014-11317: a, dorsal view; b, lateral left view; c, telson and uropods. Syntypes, MNHN IU-2014-11318: d, dorsal views; e, lateral views; f, telsons and uropods.

Bouvier (1914, 1915) distinguished his variety from Mauritius, *Axius acanthus mauritianus*, on differences in the denticulation of the median rostral ridge, the number and nature of the spines on the anterolateral margin of the carapace and cervical groove, spination of the merus of the cheliped, and ornamentation of the pleonal epimera. Fourmanoir (1955) recorded the variety from the Comores. Consistent differences from material from New Caledonia could not be detected during our examination of numerous

specimens from the western Indian Ocean. Spines on the carapace and antenna varied in number and strength, even within a small geographic range. Spination along the ventral margins of pleonal epimera 2–4 ranged from non-existent to prominent, as it does in other populations. The longitudinal ridges extending from the second transverse ridge usually carried one or two small tubercles. In some specimens from Japan a single large tubercle dominated but not in others from the same location.

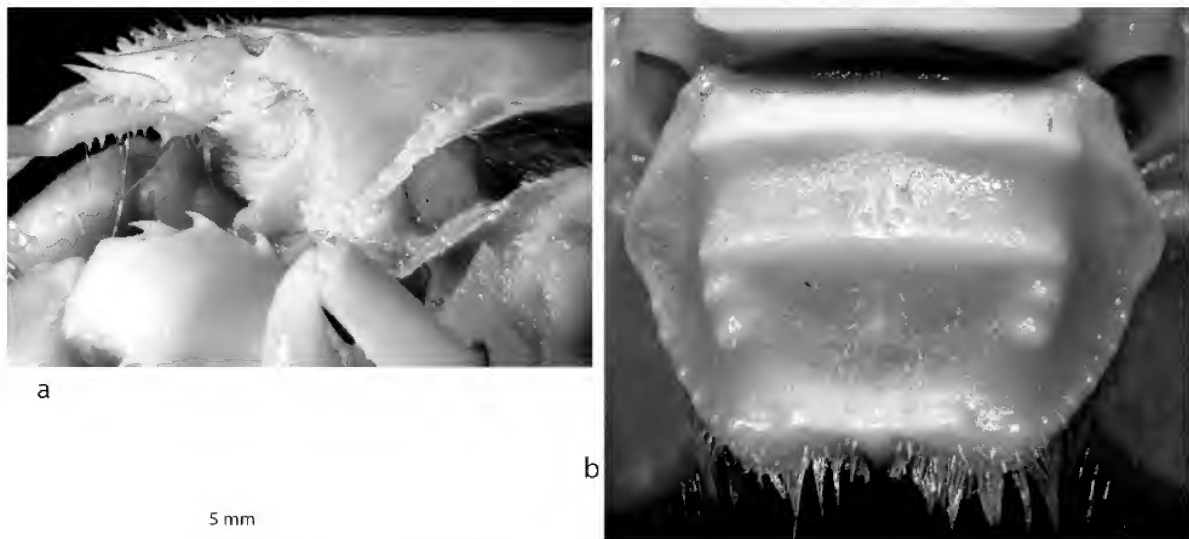


Figure 3. *Eiconaxius taliliensis* Borradaile, 1900, syntype, male, UMZC I.57590: a, lateral view; b, telson.



Figure 4. *Neaxius acanthus* (A. Milne-Edwards, 1879): a, b, Papua New Guinea (PAPUA NIUGINI stn PR195-A), MNHN unregistered, photos, A. Anker; c, d, Philippines, Looc, NHMW 25863, photos, T.-Y. Chan.

De Man (1896) was the first to apply the name *acanthus* to specimens of *Neaxius* from Sulawesi, Indonesia (as Celebes) and later from New Britain, Papua New Guinea (as Nouvelle Poméranie) (De Man, 1898, 1925a). Borradaile (1900) introduced *Eiconaxius taliliensis* for representatives from this region but soon synonymised it with *A. acanthus* (Borradaile, 1903). We examined the syntypes of *E. taliliensis* and several specimens from nearby but could not detect consistent differences between them, nor could we detect differences from individuals from Malaysia, Palau, Philippines, Taiwan or Japan. Similarly, the syntypes of *Axius acanthus mauritiana* resembled others from the western Indian Ocean no more than they did those from the western Pacific. The numbers of spines on the carapace and cheliped varied over a small range between individuals and from one side of an individual to the other, as did the expression of spines, some individuals having more prominent spines than others (see figs 1–4 and especially 5). This variability was not correlated with locality.

Sakai (2011) listed *Axius acanthus mauritanus*, *Eiconaxius taliliensis* and *Neaxius trondlei* Ngoc-Ho, 2005 in the synonymy of *N. glyptocercus*. While the synonymy of

Axius acanthus mauritanus and *Eiconaxius taliliensis* with *N. acanthus* is supported on morphological grounds, *N. acanthus* differs from *N. glyptocercus* in the many ways tabulated by Ngoc-Ho (2005). *Neaxius trondlei* from French Polynesia differs in spination from *N. glyptocercus* and *N. acanthus* for the reasons given by Ngoc-Ho (2005) (see diagnosis below).

Colour photos of live specimens indicate that the species is generally orange with stronger pigmentation on the chelipeds, anterior carapace and tailfan (Fig. 4; Anker et al., 2015: fig. 25).

Neaxius capricornicus sp. nov.

(<http://zoobank.org/urn:lsid:zoobank.org:act:0FEDB7A0-7265-4E5B-A26D-861FFB7F7B6>)

Figures 6, 8g–l

Axius (Neaxius) glyptocercus.—Poore and Griffin, 1979: 236–238 (partim), figs 8g–i.

Neaxius glyptocercus.—Tudge and Cunningham, 2002: 841.—Tsang et al., 2008: 218–219.—Robles et al., 2009: 316.—Sakai, 2011: 326–331 (partim) figs 62A, B, E.

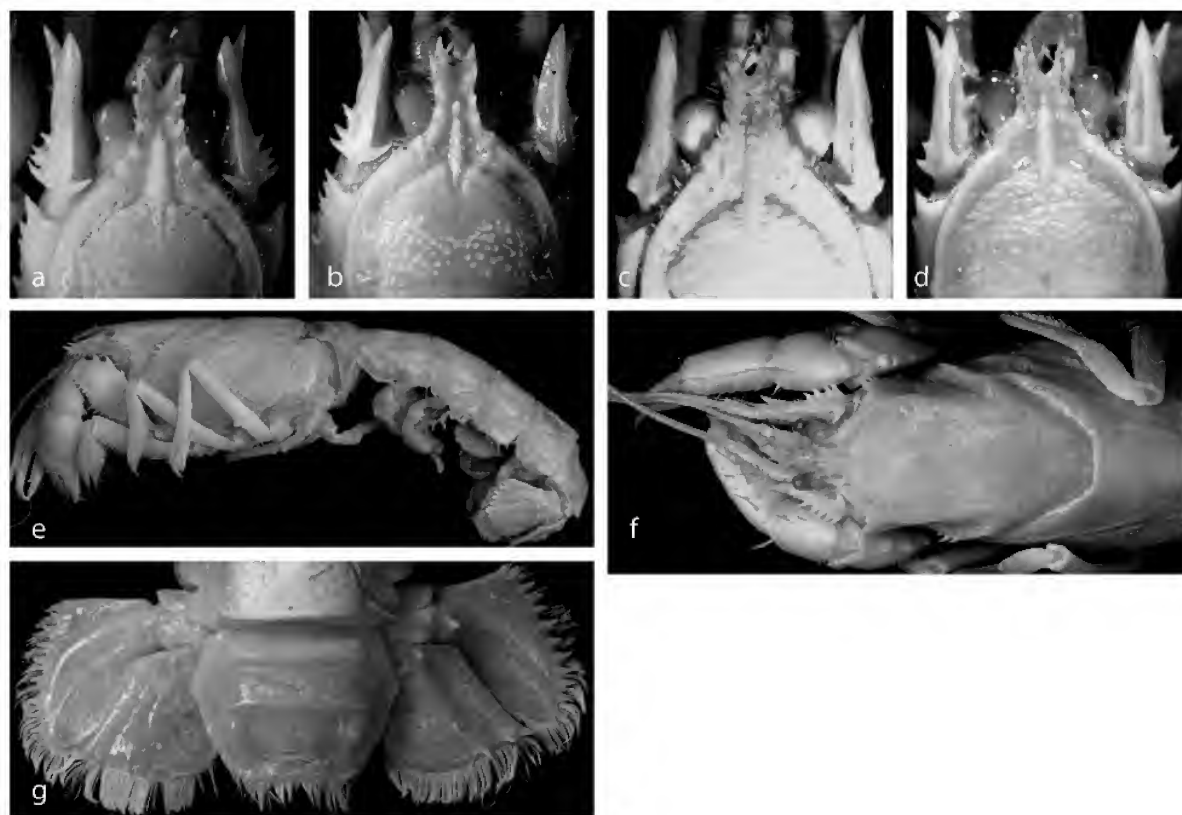


Figure 5. *Neaxius acanthus* (A. Milne-Edwards, 1879), anterior carapace: a, New Caledonia, IU 2014-22791; b, Madagascar, IU 2014-22792; c, Japan, IU 2016-8076; d, Tanzania, IU 2016-8073. Papua New Guinea, NMV J17235; e, habitus; f, dorsal carapace; g, telson and uropods. Various scales.

Material examined. Holotype. Australia, Qld, North Stradbroke I., Deanbilla Bay, Dunwich, 27° 30' S, 153° 24' E, NMV J39643 (female, 26 mm; see Tudge and Cunningham [2002]).

Paratypes. Collected with holotype. NMV J71641 (female, 23 mm); NMV J40714 (2 females, 26 mm; male, 21 mm).

Australia, Qld, North Stradbroke I., Dunwich, 27° 30' S, 153° 24' E, AM P.13723 (male, 27 mm). Capricorn Group, North West

I., 23° 18' S, 151° 42' E, AM P.10060 (female, 38 mm), AM P.11829 (female, 30 mm).

Other material. Fiji, Viti Levu, ZMH K8392 (Godeffroy No. 7430) (Sakai, 2011: fig. 62A, E) (male, 14.3 mm).

French Polynesia, Tahiti. ZMH 41226 (Sakai, 2011: fig. 62B) (male, 27 mm).

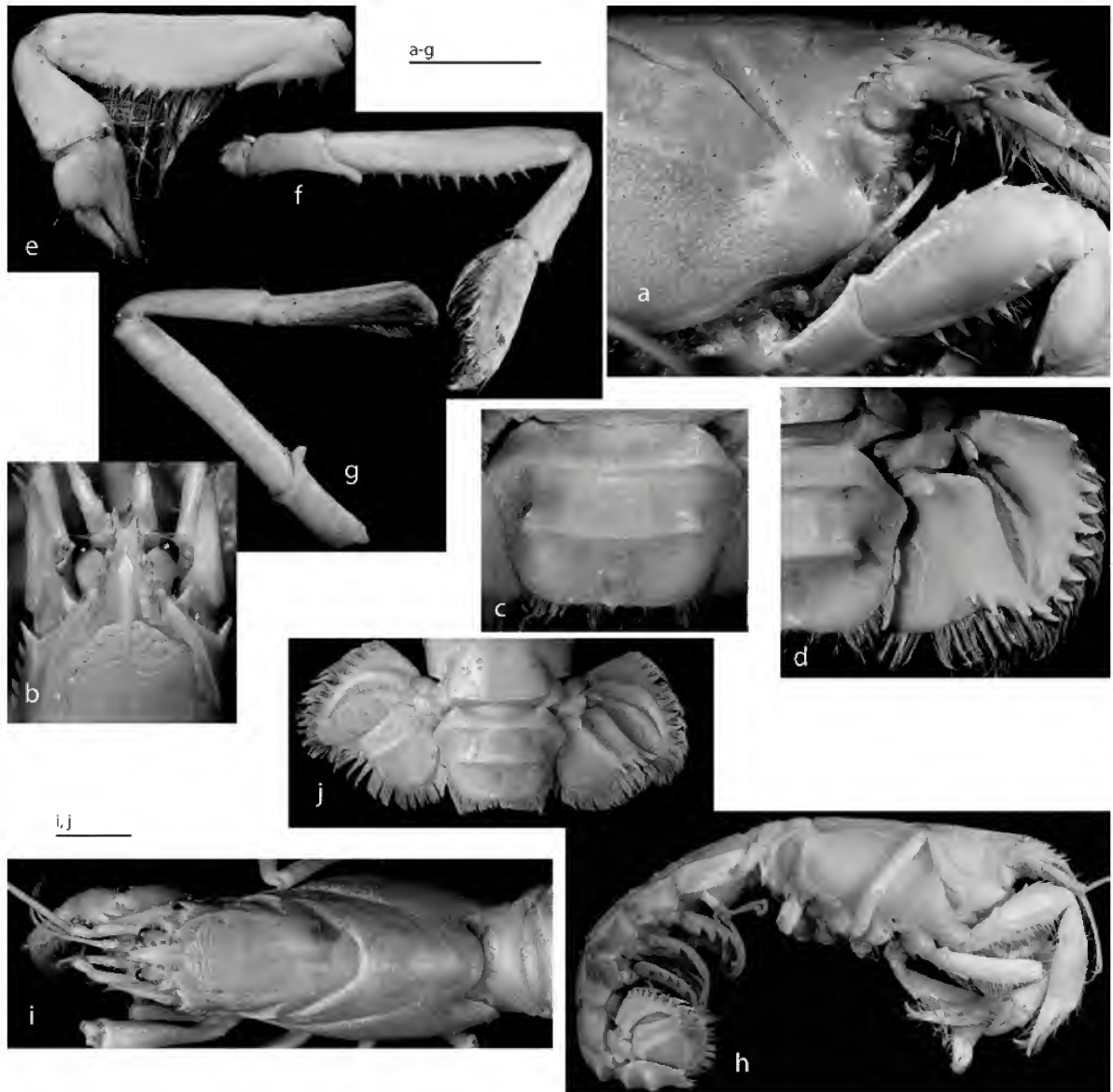


Figure 6. *Neaxius capricornicus* sp. nov., holotype, NMV J39643: a, lateral carapace, merus of cheliped; b, anterior carapace; c, telson; d, telson, right uropod; e, f, pereopods 2, 3. Paratype, NMV J71643: g, pereopod 4; h, habitus lateral; i, dorsal carapace j, telson and uropods. All pereopods, lateral faces. Scale bars = 5 mm.

Diagnosis. Carapace supra-antennal margin with anteriorly directed spine; anterolateral margin with 6 (5–7) spines, dorsalmost anterolaterally directed; branchiostegite anterior margin with 1 spine; cervical groove without spines along posterior margin. Telson 1.3–1.5 times as wide as long; tapering from widest point to posterior margin; anterior transverse ridge straight, curving laterally to reach lateral margin at its widest point; posterior transverse ridge situated at 0.5 distance between first transverse ridge and posterior margin, ends sharply rounded, almost overhanging; lateral margin with 0–2 marginal teeth; posterior face concave, with shallow median groove, smooth sublaterally. Antenna article 2 without upper-mesial spine, without lateral spine; scaphocerite with 1 mesial sharp spine, 2 (1–4) sharp ventral spines; article 4 lower margin without spines. Cheliped merus, lower margin with 5 (4–6) spines, distolateral face with row of 4 (3–5) spines. Pereopod 2 merus, lower margin with 6 (3–11) spines. Pereopod 3 merus, lower margin with 8 (4–12) spines.

Supplementary description of holotype. Rostrum with 5 pairs of erect blunt spines; sharp hiatus before smooth lateral carina; median carina with 5 tubercles; anterior gastric region rugose; cervical groove defined posteriorly by sharp carina; branchiostegal groove separating smooth cardiac region from punctate branchiostegal region. Anterolateral margin with 6 spines on right, 5 on left, first flaring laterally, longer gap between third and fourth, between fifth and sixth; anterior branchiostegal margin with 1 short spine. Pleomere 1 pleuron with 3 tubercles; pleomere 2 with 7 tubercles. Telson 1.35 times as wide as long; widest at prominent lateral

lobes, at c. 0.4 of length; tapering sharply then gradually from widest point to posterior margin; posterior margin c. 0.6 times greatest width; anterior transverse ridge at c. 0.25 length, straight, curving laterally to reach lateral margin at its widest point; posterior transverse ridge situated at 0.5 distance between first transverse ridge and posterior margin, ends sharply rounded, almost overhanging; lateral margin without marginal teeth; posterior face concave, with shallow median groove, smooth sublaterally. Antenna article 2 without mesial spine, without lateral spine; scaphocerite with 1 mesial sharp spine, 3 sharp ventral spines; article 4 lower margin without spines. Maxilliped 3 merus with 1 short, 2 longer distal spines. Cheliped coxa with 2 spines; basis with 1 spine; ischium with 3 spines; merus, lower margin with 4 spines on right, 5 on left, distolateral face with row of 3 spines, upper margin with 4 spines; carpus lower margin with 1 distal spine. Pereopod 2 coxa with 2 spines; basis with 2 spines; ischium with 3 spines; merus, lower margin with 7 spines on right, 6 on left, more proximal one minute. Pereopod 3 coxa with 2 spines; basis with 2 spines; ischium without spines; merus, lower margin spines in 2 rows: 6 spines mesially, last 3 minute, 6 laterally, last minute. Pereopods 4 and 5 without spines.

Etymology. For the Tropic of Capricorn, which marks the species' northern limit in Queensland, Australia. The name is a noun in apposition.

Distribution. Australia, Queensland, 23°S–27° 30' S; Fiji; French Polynesia.

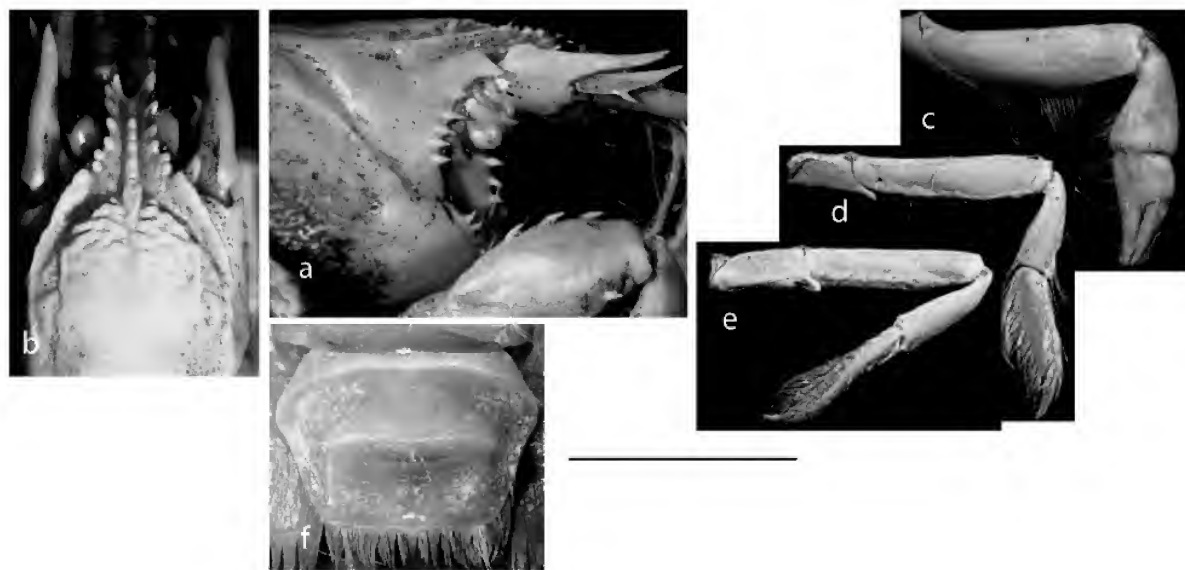


Figure 7. *Neaxius glyptocercus* (von Martens, 1868), ovigerous female, AM P.18842: a, lateral carapace, merus of cheliped; b, anterior carapace; c, pereopod 2. Female, AM P.16177: d, e, pereopods 3, 4; f, telson. All pereopods, lateral faces. Scale bar = 10 mm.

Remarks. *Neaxius capricornicus* and *N. glyptocercus* are immediately differentiated from *N. acanthus* in having a prominent supra-antennal spine on the anterior margin of the carapace, and both the cervical groove and second antenna article unarmed. *Neaxius capricornicus* differs from *N. glyptocercus* in having: 2–4 spines on the lower margin of the scaphocerite (vs. usually none, rarely 1 or 2 in *N. glyptocercus*), 3–5 spines along the distolateral ridge of the merus of the cheliped (vs. usually none, rarely one), 3–11 spines on the lower margin of the merus of pereopod 2 (vs. none), 8–12 (rarely fewer) spines on the lower margin of the merus of pereopod 3 (vs. none), one spine on the anterior margin of the branchiostegite (vs. 2 or 3) and the dorsalmost spine of the anterolateral carapace margin directed anterolaterally (vs. anteriorly).

The two species were confused by Poore and Griffin (1979) who illustrated both in their fig. 8.

Specimens from Fiji (ZMH K8392; Sakai, 2011: fig. 62A, E) and Tahiti (ZMH K41226; Sakai, fig. 62B) have 2 spines on the lower margin of the scaphocerite, 4 and 3 spines respectively along the distolateral ridge of pereopod 1 merus, 4 and 10 spines respectively on the lower margin of pereopod 2, 8 and 10 spines respectively on the lower border of pereopod 3 merus and 1 spine on the anterior margin of the branchiostegite, within the range of the Australian material.

Neaxius glyptocercus (von Martens, 1868)

Figures 7, 8m–r

Axiis glyptocercus von Martens, 1868: 613–614.—Haswell, 1882: 165–166.

?*Axiis* (*Neaxius*) *glyptocercus*.—Borradaile, 1903: 537.

Axiis (*Neaxius*) *glyptocercus*.—De Man, 1925a: 50–56, fig. 1.—De Man, 1925c: 4, 13.—Poore and Griffin, 1979: 236–238 (partim), figs 8a–f, k.

Neaxius glyptocercus.—Sakai, 1994: 200.—Sakai, 2011: 326–331 (partim), figs 61A, C–E, fig. 62F (pereopod 2 of holotype, mislabelled) (not figs 62A, B, E = *N. capricornicus*; not fig. 61B [interchanged with 62F] = *N. acanthus*; not figs 62C, D = *N. acanthus*).

Material examined. Holotype. Australia, Qld, Cape York, ZMB 2973 (described and anterior carapace figured by De Man (1925c: 50–56, fig. 1); rostrum, antenna, pereopods 2, 4, 5, pleopod 2 figured by Sakai (2011: 326–331, figs 61A, C–E, 62A, B, F).

Other material. Australia, Qld, Cape York, Fly Point, 10° 45' S, 142° 37' E, AM P.24813 (2 females, 13, 18 mm; male, 17 mm). Townsville area, 19° 16' S, 146° 49' E, AM P.16176 (male, 20 mm). Mossman, Cooya Beach, 16° 26' S, 145° 24' E, NHMW 19591 (3 females, 13.5–24.7 mm). Cannonvale Beach, near Bowen, 20° 01' S, 148° 15' E, AM P.16177 (female, 22 mm).

NT, Darwin, Lee Point, 12° 20' S, 130° 54' E, AM P.20358 (female, 21 mm). Port Darwin, 12° 27' S, 130° 48' E, AM P.15030 (male, 19 mm). Nightcliff, Darwin, 12° 23' S, 130° 50' E, AM P.18842 (ovigerous female, 28 mm).

Diagnosis. Carapace supra-antennal margin with anteriorly directed spine; anterolateral margin with 4 (5–7) spines, dorsalmost anteriorly directed; branchiostegite anterior margin with 2 or 3 spines cervical groove without spines along posterior margin. Telson about 1.3 times as wide as long; tapering slightly from widest point to posterior margin;

anterior transverse ridge straight, curving laterally to reach lateral margin at its widest point; posterior transverse ridge situated at 0.5 distance between first transverse ridge and posterior margin, ends sharply rounded, almost overhanging; lateral margin with 0–2 marginal teeth; posterior face concave, with shallow median groove, smooth sublaterally. Antenna article 2 without upper-mesial spine, without lateral spine; scaphocerite with 1 mesial sharp spine, 1 (2) sharp ventral spine; article 4 lower margin without spines. Cheliped merus, lower margin with 3 or 4 spines, distolateral face without or rarely with 1 spine. Pereopod 2 merus, lower margin without spines. Pereopod 3 merus, lower margin without spines.

Distribution. Australia: Northern Territory, E of Darwin; Queensland, Cape York to Bowen; 10° 45' S–20° S.

Remarks. Differences between *N. glyptocercus* and *N. capricornicus* were outlined above. The species is confined to north and north-eastern Australia. The holotype was photographed for us by C. Oliver Coleman and we were able to confirm the spination of the pereopods.

Neaxius trondlei Ngoc-Ho, 2005

Neaxius trondlei Ngoc-Ho, 2005: 59–63, figs 6, 7.

Material examined. French Polynesia, Marquesas Is, Ua Huka, Hane Bay (MUSORSTOM 9 stn 19), MNHN Th1419 (holotype male, 29 mm), MNHN Th1427 (paratypes: male, 30 mm; female, 21 mm). W of Haamamao Bay, MNHN Th1428 (paratype female, 13.5 mm).

Diagnosis. Carapace supra-antennal margin without anteriorly directed spine; anterolateral margin with 3 or 4 spines, dorsalmost anterolaterally directed; branchiostegite anterior margin unknown; cervical groove with 2 or 3 spines along posterior margin. Telson 1.5 times as wide as long; tapering strongly from widest point to posterior margin, posterior margin about 0.6 greatest width; anterior transverse ridge straight, curving laterally but not reaching lateral margin at its widest point; posterior transverse ridge situated at half distance between anterior ridge and posterior margin; posterolateral margin without tubercles; posterior face concave, with well-defined third transverse ridge, without pair of sublateral longitudinal ridges subtended from ends of second transverse ridge. Antenna article 2 with 1 or 2 upper-mesial spines, without lateral spines; scaphocerite with 1 mesial sharp spine, 5 sharp ventral spines; article 4 lower margin without spines. Cheliped merus, lower margin with 3 or 4 spines, lateral face without row of spines. Pereopod 2 merus, lower margin without spines. Pereopod 3 merus, lower margin without spines.

Remarks. *Neaxius trondlei* is distinguished by the unique combination of no spines on the lateral margin of the second article of the antenna and no spines on the lateral face of the cheliped or on the lower margins of pereopods 2 and 3. The species and *N. capricornicus* both occur in French Polynesia but c. 1400 km apart. They can be differentiated by the presence of spines along the cervical groove and spines on article 2 of the antenna.



Figure 8. *Neaxius acanthus* (A. Milne-Edwards, 1879), NMV J17235, male, 26 mm: a–f. *Neaxius capricornicus* sp. nov., holotype, NMV J39643: g–k. Paratype, NMV J71641: l. *Neaxius glyptocercus* (von Martens, 1868), AM P.16177: m–r. Note: a, b, g, h, m, n, dorsal and lateral views of anterior carapace; c–f, i–l, o–r, pereopods 1–4. Pereopods 1, 2 in lateral view, pereopods 3, 4 in mesial view. Scale bar = 5 mm.

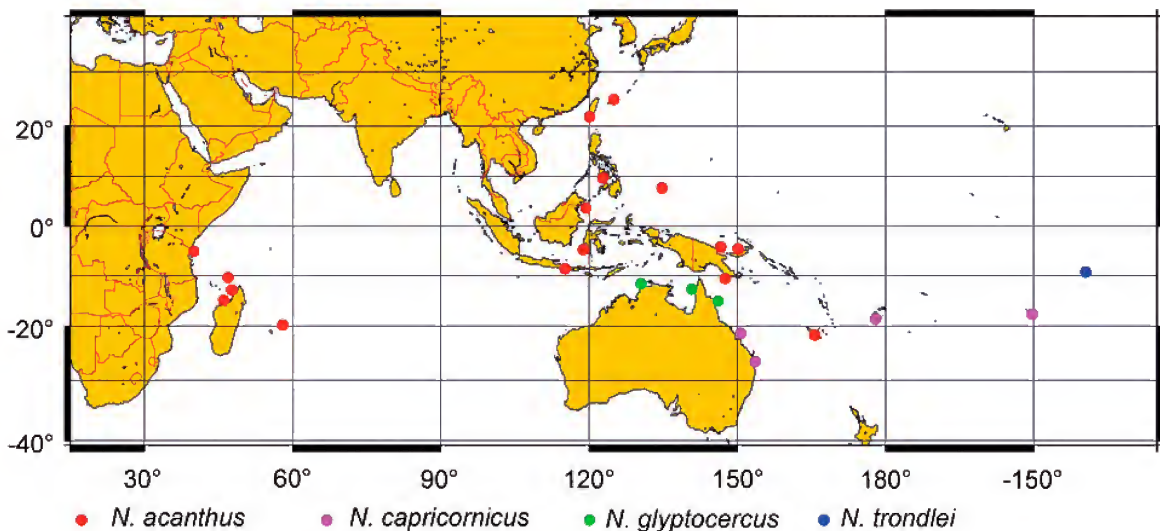


Figure 9. Distribution of four species of *Neaxius* in the Indo-West Pacific (based on material examined).

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The death adder *Acanthophis antarcticus* (Shaw & Nodder, 1802) in Victoria: historical records and contemporary uncertainty

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Abstract

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The south-eastern distributional limit of many Australian species coincides with northern, and sometimes far-eastern, Victoria. In the mid-19th century, Blandowski's Lower Murray Expedition sought to study the natural history of this area, specifically north and north-western Victoria. The expedition collected many specimens that are now registered with Museums Victoria, including species that are now extinct, extinct in the state or greatly reduced in distribution. During the expedition, a specimen of the death adder *Acanthophis antarcticus* was collected at Lake Boga in north-western Victoria. During the 20th and 21st centuries, there has been debate about whether this species persists in Victoria. We review early records of this species, including voucher specimens held by Museums Victoria, one of which we confirm as the specimen collected during Blandowski's Lower Murray Expedition. We also explore recent claims of sightings of this species in Victoria. We collate names for the death adder used by Aboriginal people in northern and north-western Victoria. Death adders undoubtedly occurred in north-western Victoria in the 19th century and were known to the Aboriginal people, but it is probable that they no longer occur in that part of the state. It is possible that death adders persist in far East Gippsland, east of the Wallagarragh River, although no substantiating material, such as photographs or specimens, has been collected in that area.

Keywords

Gerard Krefft, Blandowski Lower Murray Expedition, voucher specimen, venomous snake

Introduction

The death adder *Acanthophis antarcticus* is a distinctive and iconic venomous snake found over much of eastern and southern continental Australia, except for the cooler parts of the south-east (Cogger, 2014, fig. 1). The south-eastern limit of the species' distribution is generally accepted to be in or abutting northern Victoria and far East Gippsland. The pre-eminent national guide to the herpetofauna of Australia since the 1970s is *Reptiles & Amphibians of Australia* by Harold Cogger (1979). Early editions of this book described the species' distribution as “throughout continental Australia, except central desert regions and wetter parts of Vic and south-eastern NSW” (Cogger, 1979, p. 373), and the accompanying map included the species in far north-western Victoria. However, the latest edition (Cogger, 2014) describes this part of the species' range only as “through parts of

southern and south-eastern Australia”, and the accompanying map no longer includes north-western (or any) parts of Victoria (p. 856). There are few reliable accounts of the species' occurrence in the state (the species is listed as Data Deficient by the Department of Sustainability and Environment, 2013), and there is uncertainty about the provenance of the three specimens held by Museums Victoria that are labelled as being from Victoria. We sought to document references to death adders in Victoria from the literature, review the provenance of putative Victorian death adder voucher specimens in the collection of Museums Victoria and, lastly, review selected verbal accounts of death adders from Victoria.

Acceptable records of the death adder in Victoria

Voucher specimen from Blandowski's Lower Murray Expedition (1856–57)

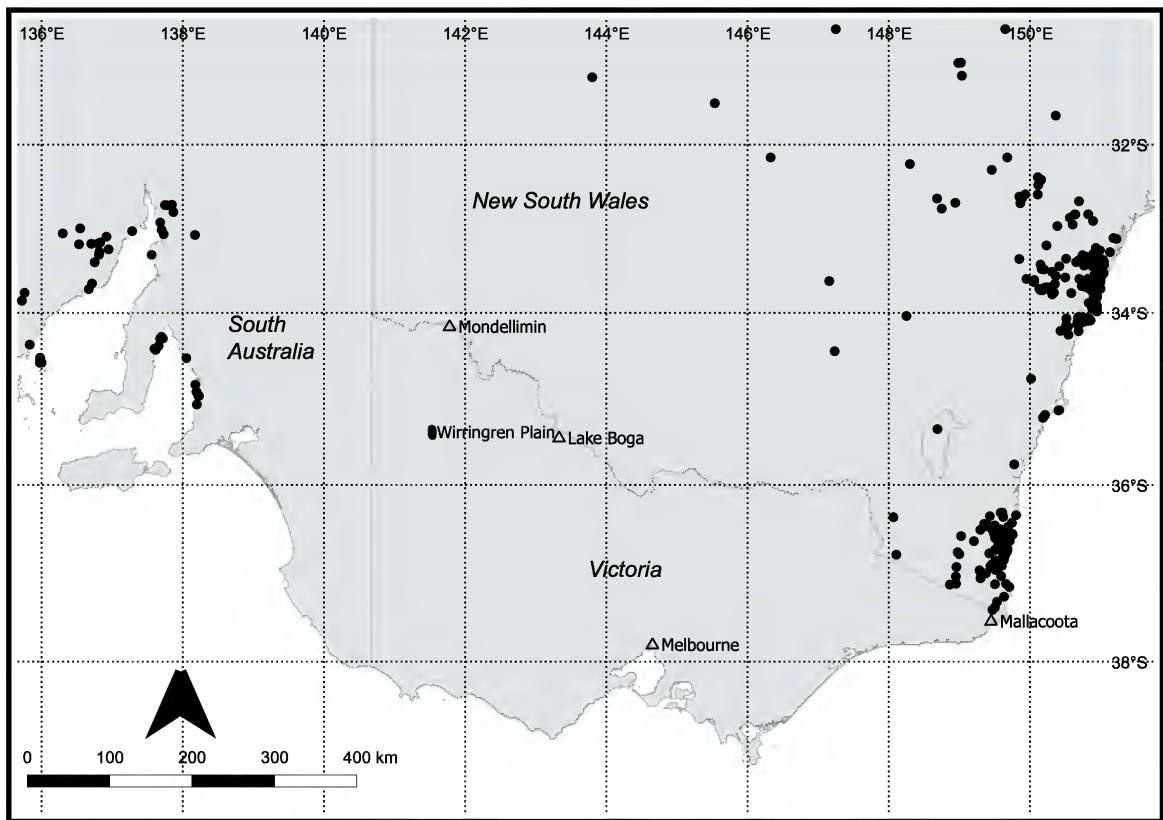


Figure 1. South-eastern Australia, showing records of the death adder *Acanthophis antarcticus* (black dots; Atlas of Living Australia, year) and key localities discussed in the text.

The occurrence of the death adder in Victoria was confirmed during Blandowski's Lower Murray Expedition in the mid-19th century. Confirmation came "from the diary of Gerard Krefft who, in 1856, drew the head and the tail of a specimen from Lake Boga" (Coventry and Robertson, 1991, p. 22; however, see below for a correction to the year of this record). Our recent re-examination of the relevant text in Krefft's narrative (which is not really a diary *per se*) hinted at the possibility of there being more information regarding this record and prompted a re-evaluation of this species in Victoria.

Krefft (c. 1858) provides a rather detailed description of the finding, capture and documentation of this snake in 1857, the day after the expedition arrived at the Lake Boga Mission Station:

Sunday Morning the 8th of March found us busy as ever for Mr Blandowski begged of us to remember the holy day we had the night before which as usual silenced all opposition. I had been up early and was busy transferring a toad to paper which I had caught when my attention was roused in repeated "queeing" (a loud noise used in the bush to call at one another). First I took no notice of it but the Captain told me to see what was wrong and so I left the hut.

I found our Cook in the deserted garden of the mission wrangling with a snake, the head of which he had secured to the ground like a sensible fellow with a forked stick. He informed me that he had been looking for some tomatoes and lifting one of the bushes he nearly touched the snake. A stick with a prongue to it was soon found and there he was.

I took charge of the reptile and told him to report to the Captain who immediately came up to the field of action and gave directions to take the snake alive. Now I have had a great deal of experience in snakes and secured many a one alive, but as the specimen in question was to all appearances a Death Adder, supplied with a poisonous sting on the end of the tail; I did not like to take it up. So after a few words with the Captain, I asked him to show me how to catch it, which he instantly did by taking hold of the snake behind the jaws. I had tied a bit of cord around the tail to prevent the snake from making use of it and so we carried the ugly customer to the hut. Mr Bl made several vain attempts to pass the snake off on myself but as I thought that he had a good grip of it, I begged to be excused. We pinned it down on a board as I set immediately to work to secure its colours while alive. I might

as well state here a fact often observed, that every snake or part of a snake, however mutilated will live until the sun goes down and though the neck had been cut through this snake lived until evening.

Our commander considered the reptile to be a new species which I doubt as it is by all appearance Brown's Death Adder. Having made a minute drawing of it I am able to describe all its peculiarities. It measured about 30' and was rather thick in proportion to its length. The head flat and the scales distributed in the same manner as in most all other Australian snakes. Of a Brown colour, all the scales on the back were divided or riveted vide sketch in the margin. The borders of the scales on the head turned upwards. The belly was of a pale pink colour with the side scales dotted with darker pink spots not unlike those which the edges of books are ornamented vide sketch. From the abdomen to the end of the tail about 5', the tail all at once becoming very thin. The specimen is now in the Melbourne Museum although much destroyed by the dirty fluid in which Mr Bl attempted to preserve his specimens.

Blandowski (1858) mentions an incident that probably relates to this encounter: "At Lake Boga I was exposed to some danger in presence of my men, by a very poisonous snake, on which I had inadvertently placed my feet" (p. 135). The statement in the final sentence of the excerpt from Krefft's narrative – that a specimen had been lodged with the Museum in Melbourne – aroused our interest. cursory inspection of the death adders in the Museum's collection immediately revealed the most promising candidate, specimen D4349 (fig. 2). The label on the jar that holds this specimen mentions a date and locality that approximates the era and localities of the Lower Murray Expedition: the "Banks of the Murray" in 1859. The Lake Boga Moravian Mission Station was established by German missionaries Brother Andrew Frederick Charles Taeger and Brother Frederick W. Spieseke on the south-eastern shore of Lake Boga in 1851 and abandoned on 27 May 1856 (Kenny, 2003, which contains a sketch of the mission location on page 104). This location is approximately seven to eight kilometres south of the Murray River, and a little over five kilometres south of the Little Murray River channel (fig. 1).

Two other features of specimen D4349 accord well with Krefft's narrative. First, the length of the snake was estimated by Krefft to be "about 30" inches (this measurement is repeated on Krefft's illustration of the Lake Boga adder, pencilled adjacent to the full-body image). Using a piece of string to run along the body of specimen D4349, we measured its total length at 728 mm (28.7 inches), consisting of 635 mm (25 inches) snout to vent and 93 mm (3.7 inches) tail length. However, the tip of the tail has been lost, either deliberately cut off or broken, since collection (fig. 3). Given Krefft's concerns about the "poisonous sting on the end of the tail", it is plausible that the tail tip was removed while the snake was being processed by Blandowski and Krefft. With a complete tail, this specimen would be very close to 30 inches in total length and the tail would be very close to the five inches mentioned by Krefft. Second, Krefft notes that "the neck had been cut through". Specimen D4349 has an obvious broad wound on the dorsal surface of the neck (fig. 4). Certainty that this is the

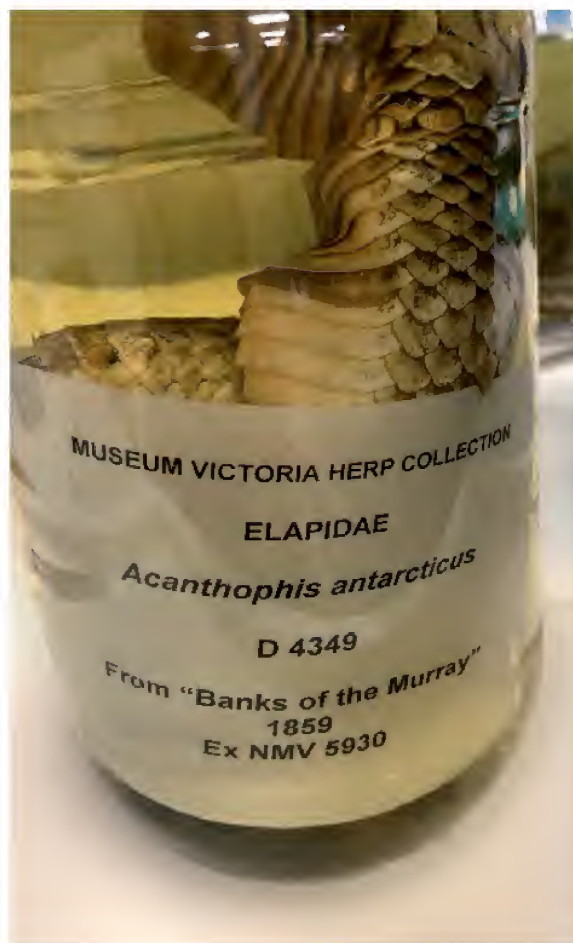


Figure 2. Specimen D4349, a death adder *Acanthophis antarcticus* in the collection of Museums Victoria.

death adder collected at Lake Boga in 1857 required careful comparison with the detailed and accurate illustration prepared by Krefft on the day the snake was captured.

Krefft's illustration of the death adder is held in the collection of the Historische Arbeitsstelle (Historical Collections department) at the Museum für Naturkunde, Berlin (reg. no. MfN, BVIII / 56). The illustration (fig. 5) is in pencil, ink and watercolour, and includes an image of the whole animal, with details of the head and tail along with some short explanatory notes. It is clearly by Krefft's hand and in his style (Stranks, in prep.).

Krefft's illustration was retained by Blandowski among the bound portfolios of illustrations assembled during his time in Australia, and it would have stayed with Blandowski during 1857 to 1859 while he was back in Melbourne after the Lower Murray Expedition. Although all of the natural history specimens collected during the 1856–57 Lower Murray



Figure 3. The truncated tail tip of death adder specimen D4349 (left) compared with the full tail tip of specimen D3579 (right).



Figure 4. Dorsal perspective of the head and neck (including neck wound) of specimen D4349.

Expedition were lodged at the National Museum in Melbourne, Blandowski retained possession of most of the illustrations and papers pertaining to the expedition (including the death adder illustration); he was eventually granted permission from the Victorian Government to retain this material for further study, and it went with him to Europe in March 1859 (T. Stranks, unpublished data).

Blandowski's portfolios returned with him to his hometown in Gleiwitz, Upper Silesia (now Gliwice, Poland) in 1860

(Darragh, 2009). They were part of the collection that stayed with Blandowski's family in Gleiwitz after he was committed to the Bunzlau mental asylum in September 1873. Not long after Blandowski's death in December 1878, his sister Clementine donated the collection to the Königlische Bibliothek zu Berlin (Royal Library, Berlin) in August 1881. The natural history-related material from the collection was eventually transferred to the Zoologisches Museum in Berlin in a series of moves in 1882, 1884 and 1885 (and has remained with that institution, which is now known as the Museum für Naturkunde; see Darragh, 2009; Landsberg and Landsberg, 2009).

We have a high-resolution version of the illustration (200 MB TIF / 17 MB JPEG; fig. 5), which allows the fine detail of the illustration and annotations to be seen. Consequently, we can read Blandowski's handwriting in pencil with "Lake Boga" (bottom left), "sehr giftig, nur 2 bis 2 1/2 'lang'" (very poisonous, only 2–2.5 feet long; bottom right), and Krefft's handwriting, with "Snake A" and "30 inches" (centre right) and "Death Adder" (bottom centre).

On 17 July 2017, we compared Krefft's illustration with the following six specimens of death adder from the collection at the Melbourne Museum: D3579, D51857, D15392, D15394, D76869 and D4349. These specimens were chosen because their labels suggested that they might have come from Victoria, or their collection locality is not mentioned on the label of the receptacle in which they are kept at the Museum (i.e. all the other death adder specimens in the Museums Victoria collection are labelled as being collected from other states). Using a stereomicroscope, we examined details of scalation and colour, primarily on the ventral surface of the heads of each snake, comparing them to the illustration. Scale and colour were highly variable between specimens. D4349 was the only exact match for the illustration of the death adder from Lake Boga, confirming beyond doubt that this was the specimen collected in 1857 by Blandowski, Krefft and the expedition's cook (fig. 6, which includes images of the two



Figure 5. Illustration by Gerard Krefft of the death adder collected at Lake Boga in north-western Victoria on the 8 March 1857. (Photograph by Rebecca Carland; Museum of Natural History Berlin. Historical collection of pictures and writings. [Sigel: MfN, HBSB.] Bestand: Zool. Mus. Signatur: B VIII/56.)



Figure 6. Ventral view of the head scales of Death Adder specimens from Melbourne Museum, and close up of Gerard Krefft's illustration of the ventral head scales of the Death Adder collected at Lake Boga in 1857 (bottom right). Top left is specimen D3579. Top right is D51857. Bottom left is D4349.

other death adder specimens with “Victoria” on their labels, allows comparison of the three specimens with Krefft’s illustration and shows that only D4349 is a precise match for the snake collected at Lake Boga in 1857).

There are minor discrepancies around the dates of this record. Coventry and Robertson (1991) state the year of the record as 1856; however, this was the year that Blandowski’s Lower Murray Expedition commenced (departing Melbourne on 6 December 1856; Allen, 2009a; Darragh, 2009), and Krefft’s narrative is clear that the death adder was found and captured on 8 March 1857. Specimen D4349 is labelled in the old National or Public Museum register as dating from 1859. Although two years later than the collection date of the Lake Boga adder, it is plausible that either the final digit of the date was transposed incorrectly (the handwriting of the digit 7 in the museum register resembles a 9 to some degree) or – more likely – that the more recent date represents the date the specimen was registered or catalogued at the museum. Many of the collections from Blandowski’s Lower Murray Expedition in the Museums Victoria collection were simplistically labelled and registered as coming from the “Junction of the Murray and Darling Rivers” (the expedition’s official destination), even for specimens collected considerable distances from the location (Wakefield, 1966); the date given in the register is often the date of registration rather than the date of collection (discussed by Wakefield, 1966). The collection from Lake Boga and Mondellimin, the expedition’s camp (now known as Chaffey Landing, near Mildura; fig. 1), would have arrived in Melbourne by mid-1857. By this stage, the Public Museum was under Frederick McCoy’s control, and was located in the north wing of the Quadrangle Building at the University of Melbourne. The material may have been stored there, largely unworked, until further sorting took place in readiness for the Museum’s first collection registration system in c.1858–1859.

Alternatively, perhaps due in part to his feud with McCoy (Allen, 2009a), Blandowski was loath to hand over specimens to the Museum, instead transferring them to his private lodgings (Pescott, 1954, cited in Wakefield, 1966). Allen (2006) states:

In 1858, Blandowski received a letter from the Surveyor-General requesting him to surrender all drawings and memoranda relating to the Natural History of the country, made during the period he held an appointment in the Government Service. Blandowski’s reply states his position, “I deny ... the justice of this demand, and as I regard these papers and drawings my private property, I must decline to allow them to pass out of my hands” (Paszowski 1967:160, quoting Blandowski letter of 23 November, 1858) (p. 33).

Thus, it is plausible that Blandowski begrudgingly released specimens over the period spanning his return from Mondellimin and his departure for Germany in 1859, perhaps resulting in the specimen now labelled as D4349 not entering the collection until 1859.

Interestingly, Krefft perpetuates two myths about snakes in his narrative. Krefft was a knowledgeable zoologist, so his belief that it is “a fact often observed, that every snake or part

of a snake, however mutilated will live until the sun goes down” is odd for an experienced collector who had presumably killed and prepared many reptiles. Less surprising (for the era) is Krefft’s belief that death adders have “a poisonous sting on the end of the tail”. By the mid-19th century, the European colonisers still had much to learn about the biology of many Australian species, and the specialised tail of the death adders was clearly believed to be a venomous adjunct to the snake’s fangs (the tail tip of death adders usually has a terminal spike that resembles a venomous sting; fig. 3). Death adders use their specialised tails to lure small vertebrate prey, and early observers who witnessed the outcome for animals lured to the snake’s tail may have believed that the tail indeed contained a venomous sting. However, Krefft later corrected this fallacy in his book on Australian snakes, where he states that the tip of the death adder’s tail, “which is so much dreaded by many persons, is neither a weapon of attack or defence” (Krefft, 1869, p. 80).

Intriguingly, the text on the receptacle holding specimen D4349 is a precise match for the words used by another natural history illustrator from that period in relation to some snake specimens. Ludwig Becker was the artist and naturalist who accompanied the Burke and Wills exploring expedition in 1860–61, and he wrote the following letter (held in the collection of the State Library of Victoria) to Dr John Macadam (Honorary Secretary of the Royal Society of Victoria’s Exploration Committee) while the expedition was staying at Camp 15 at Swan Hill on 8 September 1860, regarding a bottle of three snakes to be donated to the Museum by Dr Benjamin Gummow (doctor at Swan Hill from 1857–72):

Camp at Swan Hill

Sept. 8. 1860

To Dr J Macadam MLA

Hon. Secretary

Royal Society in Victoria.

PS. By this mail I have the honor to forward to you a bottle containing 3 snakes presented to the Museum by Dr Gummow [sic] of Swan Hill. The 2 larger snakes were found near Swan Hill on the Banks of the Murray, the small one in the Mallee Scrub, 40 miles from Swan Hill, but still in Victoria.

I have etc.

L Becker.

The words “Banks of the Murray” is a match with the details in the specimen register for D4349, although it is plausible that “Banks of the Murray” may have been like “the Junction of the Murray and Darling Rivers”, a term used in that era to describe various locales in northern Victoria close to the Murray River (see Wakefield, 1966).

Becker does not appear to have illustrated these preserved specimens from Swan Hill (or illustrated any death adder from the Burke and Wills expedition), but he does provide another illustration and short accompanying note of a live specimen of death adder (unknown locality and date, but presumably from around the same region and period):

Deaf [sic] adder, 1/5 nat. size, full grown, whole length exactly 3 feet, greatest diameter 2 ½ inches, colour of upper part of head and body: brown, with transverse bands (about 30) of a lighter tint; under part pale yellow. Scales spined. Spine on the end of tail sometimes half an inch long. The one I killed crossed the road in front of my horse and moved slowly towards the grass, and when attacked by me with a stick, rose in self defence, resting upon the broadest part of his body. L. Becker.

Becker's pencil, ink and watercolour illustration and handwritten note can be seen online at the website Caught and Coloured: Zoological Illustrations from Colonial Victoria (Kean et al., 2006). Becker later transformed his illustration into a beautiful lithograph for McCoy's *Memoirs of the Museum*; this was never published, but the illustration eventually appeared as Plate 12 in the *Prodromus of the Zoology of Victoria* (McCoy, 1878). Becker's information provided much of the source information for McCoy's account of the species, which McCoy said was restricted to "hot tracts near the Murray River" (p. 12).

William Lockhart Morton's death adder record (1861)

William Lockhart Morton provided an account of finding and killing a death adder on the eastern edge of the Big Desert, west of Pine Plains and Patchewollock, in July 1861 (the locality description by Morton notes entering Wirringren Plain, then turning west, crossing the plain over four miles before he began to "mount the acclivity of the sandy desert country" where he found the death adder "on the sloping bank on a spot exposed to the warm morning sun"; Morton, 1966, p. 43). After killing the snake, Morton cut off the "tail-like prolongation", which he later examined under a microscope, noting that "the reputed sting appears blunt, and though a dark line runs along it, giving it seemingly the character of a tube, no opening at that point can be detected. It is by its bite that the death-adder proves so instantaneously destructive to animal life" (Morton, 1966, p. 44). Morton notes that his "companion, who had resided for eight years in South Africa, remarked that this specimen bore a strong resemblance to the puff-adder of that country" (p. 43).

Other claimed Victorian records of the death adder

Voucher specimens

As well as the Lake Boga adder, there are two death adder voucher specimens in the collection of Museums Victoria that are labelled as being from Victoria (fig. 6). One of these specimens (D51857) was given to the Museum by Steve Wilson but was not collected in Victoria (email from Steve Wilson to JM, 16 May 2017).

According to the hand-written specimen register, death adder specimen D3579, with the locality listed only as "Victoria", was lodged with the Museum by "Prof. Halford 23/7/1878". George Britton Halford was a British anatomist and physiologist who founded the first medical school in Australia at the University of Melbourne. From 1866, Halford conducted research in Melbourne on the effects of snake venom, inducing snakes to bite dogs, cats and pigeons

(Hobbins, 2013). After experimenting with animals, by 1868 Halford (who believed that venom comprised living germinal matter) began trials using injected ammonia as an antivenom (Hobbins, 2013). This treatment remained in use for some time (*The Victorian Naturalist*, Vol. IX, No. 1, 1892, p. 2, under 'Exhibition of Specimens' reports a death adder collected at Mondulval, NSW, "after having bitten Mr. J. M. Simson, of Toorak, who was successfully treated with strychnine and ammonia"). Given his research using Australian elapid snakes, it is probable that specimen D3579 was in Halford's possession for this purpose. In his account of the death adder in the *Prodromus of the Zoology of Victoria*, McCoy (1878) states that: "a large dog bitten by a captive Death Adder in one of Dr. Halford's experiments was dead in 18 minutes", confirming that at least one death adder was used by Halford. It is likely that Halford was supplied with snakes by others. Even in the 19th century, death adders had a restricted distribution in Victoria, and it is unclear whether or not specimen D3579 was collected in Victoria.

Further references to Victorian death adders in the literature

References to death adders in Victoria in the literature show that death adders were an accepted component of the Victorian fauna by the late 19th century; however, these references do not add any more specific, substantiated records than those discussed above. Krefft (1866) again mentions the death adder collected during Blandowski's Lower Murray Expedition by stating: "of this highly venomous snake, I obtained but a single specimen at Lake Boga; it brings forth about 10 or 12 young" (p. 31). McCoy (1878) states that death adders were "not found in the southern parts of Victoria, but common in the hot tracts near the Murray" (p. 12). A poster presenting the *Dangerous Snakes of Victoria*, produced in 1877 by the Museum and the Education Department for distribution to all Victorian schools and railway stations, features the death adder along with another four species of well-known venomous snakes that remain abundant in Victoria (fig. 7). A second edition of this poster, containing the same five species with updated illustrations that were more life-like, was produced in the 1890s (<https://museumvictoria.com.au/caughtandcoloured/deadoralive.aspx>). McCoy (1867) notes that, in Victoria the death adder was "confined to the northern boundary" (p. 182). Le Souef (1884) lists the "Death or Deaf Adder" (p. 87) in his *Catalogue of Victorian Fauna*. Soon after this, Le Souef (1887; based on a trip undertaken in December 1886) writes that near Lake Hindmarsh, "a farmer lately ploughed up six death adders when ploughing up new land, but they were not numerous, and we saw none, although a good lookout was kept ..." (pp. 44–45). It is possible that other snake species that occur in this area – in particular the Bardick *Echiopsis curta* – could be mistaken for death adders because they look superficially similar when posing defensively. However, given the relative proximity of this area to where Morton (1966) recorded a death adder in 1861, it is not out of the question that farmers ploughing this new land did indeed encounter death adders.

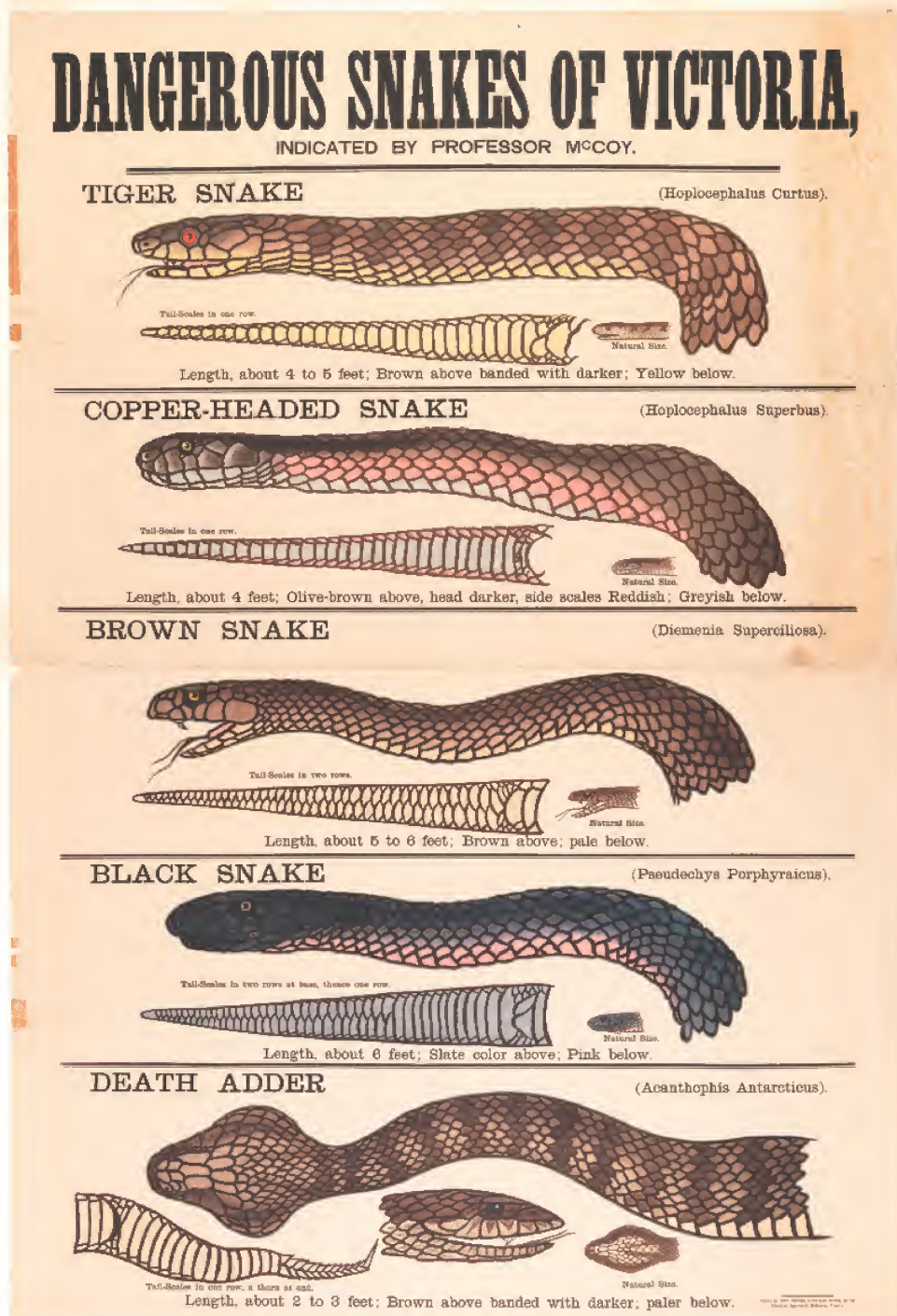


Figure 7. First edition of the *Dangerous Snakes of Victoria* poster, produced in 1877.

Early in the 20th century, French (1901), commenting on the fauna of the Victorian Mallee, notes that the death adder is one of the snakes of the region (although he did not encounter this species during the trip that forms the basis of his article) but “appears to be rather rare in Victoria” (p. 14). At around the same time, Best (1901) notes that “with respect to snakes, at our last meeting Mr. Le Souëf mentioned that in the Mallee the Death Adder was more numerous than is generally supposed, as owing to its sluggishness it is often passed over” (p. 93). Kershaw (1927) states that the death adder “in Victoria, is restricted to the dry areas of the north-west” (p. 337). Worrell (1963) states that death adders are “rare in Victoria” (p. 108); identical words are used by Gow (1976). Wilson and Knowles (1992) suggest that the species “penetrates Vic. only in far east and north-west” (p. 379), and their accompanying map reflects that statement. Wilson and Swan (2013) provide a distribution map but no description of the species’ range; however, they do report the death adder’s current status in Victoria (Data Deficient), with the Department of Sustainability and Environment (2013) being the source for this listing.

Aboriginal knowledge of the death adder in Victoria

Blandowski and Krefft worked with Aboriginal people during the 1856–57 Lower Murray Expedition (engaging them as guides, collectors and sharers of knowledge; Allen, 2009b), and at least one of the groups they encountered along the Murray River knew of the death adder. On his illustration of the death adder from Lake Boga, Krefft has added a note at the bottom about its Koorie name: *Pellettoak – Yarree Yarree*. *Pellettoak* was the animal name provided by the Yarree Yarree [Nyeri Nyeri] people who worked with the Blandowski Lower Murray Expedition at Mondellimin from April to December 1857. Blandowski and Krefft were in the practice of showing various animal illustrations to local Aboriginal people along the way, trying to gather native names for particular species (Stranks, in prep.). *Pellettoak* appears to be a specific name for death adder (as opposed to a more generic word for snake such as *Cournvil* or *Cumvill*) recorded from the Yarree Yarree. This indicates that the species was known in the Mondellimin area at the time the expedition visited, although no specimens were collected there.

Krefft gave a talk on the “vertebrated animals” (he discussed mammals only) from the “Lower Murray Expedition” to the monthly meeting of the Philosophical Society of NSW on 10 September 1862 (reported in the Sydney Morning Herald, 24 October 1862, page 2). This was followed by a continuation of the former paper – a talk on the reptiles, amphibians and fishes from the Lower Murray Expedition to the monthly meeting of the Philosophical Society of NSW on 16 September 1863 (meeting report in the Sydney Morning Herald, 21 September 1863, page 13). In this second talk, the newspaper reports Krefft stating: “The Death Adder (*Acanthophis antarctica*) [sic], not very common, as I have never seen but one single individual at Lake Boga; there is no difference in the coloration of this snake from those inhabiting the east coast; the natives [at Mondellimin] never brought one though high

rewards had been offered” (p. 13). It is notable that the Aboriginal people did not collect a specimen of the death adder during the eight months that the expedition spent at Mondellimin. Perhaps the Aboriginal people could not find the species, or would not collect it because it was venomous and dangerous, or there was a cultural consideration such as a taboo that prevented them from harming or killing it.

It does not appear that Blandowski and Krefft worked with any Aboriginal people during their relatively brief stay Lake Boga in March 1857, so there is no record of a Koorie name for the species there. Curiously, however, there is another reference to the death adder at Lake Boga. Mr A. Chas. Stone worked as the baker at Lake Boga for more than 18 years, and was in close contact with the “Lake Boga tribe”, known as Gourrmjanyuk (meaning “along the edge of trees”; Stone, 1911, p. 433), from about 1890 to 1910. He published a paper on The Aborigines of Lake Boga (Stone, 1911) that has a list of Koorie names for animals, including ten varieties of snake, with the name “Llerk” for “Deaf Adder” (p. 446, noting the frequently used – and technically erroneous – variation on the common name). This paper was a primary source for the Wemba Wemba Dictionary compiled by linguist Luise Hercus in the 1960s (Hercus, 1992); she has listed an alternative spelling of “Lirrk” for death adder (p. 106).

Claimed sightings of death adders in Victoria in recent decades

Most claims of sightings of death adders in Victoria in the late 20th and early 21st centuries have been from either the far north-west or from the eastern tip of the state. After two credible reports from beside the Murray River in the far north-west, in 2005 two of us (PR and NC) led a brief survey in the area. Instead of death adders, that survey resulted in the capture of a snake previously unknown from Victoria: *De Vis’ Banded Snake* *Denisonia devisi* (Clemann et al., 2007). It appears that those most recent claims of death adders in the riverine area surveyed by Clemann et al. (2007) were actually mis-identified *De Vis’ Banded Snakes*.

In far south-eastern New South Wales there are death adder records east of the Princes Highway in Nadgee State Forest, less than one kilometre from the border with Victoria (Atlas of NSW Wildlife, accessed online, 28 May 2017; Swan et al., 2004; fig. 1). Most (but not all) claims of death adders in far East Gippsland are from east of Mallacoota Inlet. One of us (BodB) spent much of her life in Mallacoota, observing snakes in that area. BodB’s father – an experienced naturalist – has seen what he believes to be death adders in that area on two occasions; both observations, and the majority of others she has heard of, including some recent (2016) reports, were east of the Wallagaraugh River. The few potential sightings she is aware of that occurred west of the Wallagaraugh all occurred in the 1980s. No substantiating material such as photographs or a voucher specimen have been produced from eastern Victoria.

Death adders possess traits that predispose them to population losses (Reed and Shine, 2002). Because Victoria is the southern extreme of this species’ range, it is here that declines are particularly likely. Land use changes and the

introduction of stock animals and exotic predators associated with the push into northern Victoria by European people had a profound impact on native fauna, resulting in the extinction of some mammals (Menkhorst, 2009). These impacts were already evident to Krefft in the 1850s, and it is sobering to acknowledge that the ecocidal impacts of European incursion proclaimed by Krefft 160 years ago (Kean, 2009; Menkhorst, 2009) continue to this day. As well as the losses of mammals, it is probable that around this time there were deleterious impacts on various reptile species. Frequent burning of native vegetation on public land in the Victorian Mallee has resulted in changes to the fauna (Robertson et al., 2012); both the Mallee and far East Gippsland are currently subject to frequent fuel reduction burning, and death adders may be particularly susceptible to fire (McDonald et al., 2012; Smith et al., 2012).

The Mallee region is popular with natural historians, particularly ornithologists and herpetologists, and the fact that, despite the frequent activities of these people, no reliable death adder records have been produced in north-western Victoria since the mid-19th century suggests that this species no longer occurs in that part of the state. However, due to their lower energetic needs, some reptile species may persist in small isolated areas. The part of Victoria east of the Wallagaroogh River is comparatively under-surveyed, and consequently, it is not entirely out of the question that death adders persist in the far east of the state.

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Diversity in Australia's tropical savannas: An integrative taxonomic revision of agamid lizards from the genera *Amphibolurus* and *Lophognathus* (Lacertilia: Agamidae)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:22334107-0784-466E-8288-D6E29F87F6E2>)

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Abstract

Melville, J., Ritchie, E.G., Chapple, S.N.J., Glor, R.E. and Schulte II, J.A. 2018. Diversity in Australia's tropical savannas: An integrative taxonomic revision of agamid lizards from the genera *Amphibolurus* and *Lophognathus* (Lacertilia: Agamidae). *Memoirs of Museum Victoria* 77: 41–61.

The taxonomy of many of Australia's agamid lizard genera remains unresolved because morphological characters have proved to be unreliable across numerous lineages. We undertook a morphological study and integrated this with a recent genetic study to resolve long-standing taxonomic problems in three genera of large-bodied Australian agamid lizards: *Amphibolurus*, *Gowidon* and *Lophognathus*. We had broad geographic sampling across genera, including all currently recognised species and subspecies. Using an integrative taxonomic approach, incorporating mitochondrial (*ND2*) and nuclear (*RAG1*) genetic data, and our morphological review, we found that both generic and species-level taxonomic revisions were required. We revise generic designations, creating one new genus (*Tropicagama* gen. nov.) and confirming the validity of *Gowidon*, giving a total of four genera. In addition, we describe a new species (*Lophognathus horneri* sp. nov.) and reclassify two other species. Our results provide a significant step forward in the taxonomy of some of Australia's most iconic and well-known lizards and provide a clearer understanding of biogeographic patterns across Australia's monsoonal and arid landscapes.

Keywords

Agamid lizards, *Amphibolurus horneri* sp. nov., *Lophognathus*, *Gowidon*, *Tropicagama* gen. nov., integrative taxonomy, Australia, monsoon tropics

Introduction

Tropical savannas constitute one of Earth's major biomes, covering 20–30% of the land surface (Myers et al., 2000). Australian tropical savannas are particularly important because they are the largest and least modified tropical savanna woodlands in the world, comprising approximately 25% of the Earth's remaining savannas that are in good ecological condition (Woinarski et al., 2007). The Australian monsoonal tropics, which span the northern third of the continent, are home to a major component of biodiversity, with some areas, particularly the sandstone escarpments, having similar biodiversity levels to Australian rainforests (Bowman et al., 2010). Yet, only recently has research started to uncover unexpected levels of diversity and phylogeographic structure across the monsoonal tropics (Melville et al., 2011; Moritz et

al., 2016; Oliver et al., 2014; Potter et al., 2016; Smith et al., 2011). As a result of these research findings, the current taxonomy in many groups does not reflect actual species diversity.

One lizard group that is in immediate need of a taxonomic revision is the large-bodied agamids of the tropical savannah woodlands. Despite their ubiquity and ecological significance in this biome, major taxonomic problems characterise the group at both the generic and the species levels. Molecular work suggests major taxonomic problems within *Amphibolurus*, *Gowidon* and *Lophognathus* (Hugall et al., 2008; Melville et al., 2011; Schulte et al., 2003). Melville et al. (2011) identified a clade containing five species in three genera: *Amphibolurus muricatus* (White, 1790), *A. norrisi* Witten and Coventry, 1984, *A. burnsi* (Wells and Wellington, 1985), *L. gilberti* Gray, 1842, and *Chlamydosaurus kingi* Gray, 1825. According to

Table 1. Current taxonomic designations of Agamidae genera under revision, including details of synonyms and primary types, from Department of the Environment and Energy (2014). All types have been examined for morphological analysis, except those where they are presumed lost or status unknown.

Species plus junior synonyms	Described	Details of types
1. <i>Amphibolurus muricatus</i>	[White (1790)]	BMNH 1946.9.4.44
<i>Lacerta muricata</i>	White (1790)	BMNH 1946.9.4.44
<i>Agama jaksoniensis</i>	Cloquet (1816)	RMNH 3117
3. <i>Amphibolurus norrisi</i>	Witten and Coventry (1984)	NMV D51499
4. <i>Chlamydosaurus kingii</i>	Gray (1825)	Type presumed lost.
5. <i>Amphibolurus burnsi</i>	[Wells and Wellington (1985)]	AM R 116981
6. <i>Lophognathus gilberti</i>	Gray (1842)	BMNH 1946.8.28.69
<i>Redtenbacheria fasciata</i>	Steindachner (1867)	Type not found.
<i>Physignathus incognitus</i>	Ahl (1926)	ZMB 30086
<i>Physignathus gilberti centralis</i>	Loveridge (1933)	MCZ 35207
7. <i>Gowidon longirostris</i>	[Boulenger (1883)]	BMNH 1946.8.12.64-65, 1946.8.28.73
<i>Physignathus eraduensis</i>	Werner (1909)	Status unknown
<i>Physignathus longirostris quattuorfasciatus</i>	Sternfeld (1924)	SMF 10366
8. <i>Gowidon temporalis</i>	[Günther (1867)]	BMNH 1946.8.12.73/63, 1946.8.28.72
<i>Lophognathus lateralis</i>	Macleay (1877)	AM R31882
<i>Lophognathus labialis</i>	Boulenger (1883)	BMNH 1946.8.12.72, 1946.8.12.63

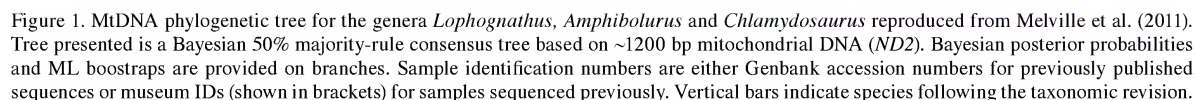
Note: BMNH, British Museum of Natural History, London; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Holland; AM, Australian Museum, Sydney; NMV, Museum Victoria, Melbourne; ZMB, Zoologisches Museum, Universität Humboldt, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, United States; SMF, Senckenberg Naturmuseum, Frankfurt-am-Main, Germany.

these results, the frill-necked lizard (*Chlamydosaurus kingii*), which has remained monotypic since its description, belongs to this clade, despite its stunning morphological distinctness. Further complicating these results is the possibility that *L. gilberti* is actually a species complex. Molecular work (Melville et al., 2011; Schulte et al., 2003) and field observations (Melville, unpublished data) led to the hypothesis that a number of populations that have been relegated to *L. gilberti*'s synonymy (Table 1, e.g. *Physignathus gilberti centralis* Loveridge 1933) may represent a valid species.

There has been a complex taxonomic history for the genus *Lophognathus*, which was originally erected for a single species (*Lophognathus gilberti*), with the inclusion of multiple species at different times, including *Amphibolurus burnsi* (Wells and Wellington 1985), *Gowidon longirostris* (Boulenger, 1883) and *G. temporalis* (Günther, 1867). The current catalogue (Department of the Environment and Energy, 2014) lists one species in *Lophognathus* (*L. gilberti*) and two in *Gowidon* (*G. temporalis* and *G. longirostris*), although a formal revision of the generic placement of *G. temporalis* into *Gowidon* has not occurred. Molecular work

suggests that *G. temporalis* and *G. longirostris* are not closely related to *L. gilberti*, and that *A. burnsi* is more closely related to *Amphibolurus*, with more recent publications reflecting this placement (e.g. Wilson and Swan, 2017). Based on this confusing taxonomic history and that the morphological characters previously used to define *Gowidon*, *Lophognathus* and *Amphibolurus* do not seem to be diagnostic, a complete review of these species is required.

We undertook a morphological study and an integrative taxonomic review of the genera *Gowidon*, *Amphibolurus* and *Lophognathus* species from northern Australia, incorporating results from the most recent molecular study (Melville et al., 2011). We examined all primary types for the study species, including junior synonyms, and conducted detailed morphological analyses using additional museum specimens that included many of the specimens sequenced in the molecular study (Melville et al., 2011). This comprehensive review of these genera provides a complete taxonomic revision and contributes significantly to our understanding of generic and species-level diversity in the Australian tropical savannas.



Materials and methods

Morphology

Primary types, including all junior synonyms (Table 1), were examined for morphological analysis and taxonomic revision. We also examined additional museum specimens for a morphological analysis of all species currently belonging to *Lophognathus* (see Supplementary Appendix S1 for details). Ten morphometric characters were measured using calipers for all specimens examined: snout–vent length (mm), tail length (mm), upper hindlimb length (proximal hindlimb; mm), lower hindlimb length (distal hindlimb; mm), hindfoot length to end of fourth toe (autopod hindlimb; mm), head length (mm), head width at widest point behind ear (mm), head depth at deepest point between eyes and ears (mm), number of femoral pores and number of preanal pores. In addition to these morphometric measurements, specimens were examined for scalation patterns, colour patterns and other synapomorphies.

Univariate and multivariate analyses were used to examine differences in the morphometric characters between the species. We used SYSTAT Version 10.2 (SYSTAT Software Inc., Richmond, California, USA) for analyses. Before analysis, all morphological variables were regressed against snout–vent length and the residuals were used for subsequent analyses to remove the effect of body size. First, all ten morphometric characters were analysed using analysis of variance with multiple comparisons (Tukey's procedure). Then, principal components analysis was used to reduce the dimensionality of the morphological data (FACTOR procedure of SYSTAT). Principal components were extracted from a correlation matrix of the raw data. Principal components were named by the correlations of the original variables to the principal component; correlations with absolute values greater than 0.5 were considered important. Resultant principal components were explored using analysis of variance with multiple comparisons (Tukey's procedure) to determine whether there were interspecific differences in morphometric characters.

Species delimitation assessment

We used an integrative taxonomic approach for species delimitation assessment by following the principle that as many lines of evidence as available should be combined to delimit species (Miralles and Vences, 2013), which has been successfully used in Australian dragon lizards (Melville et al., 2014). We first used the mtDNA phylogenetic tree in association with the nuclear tree to determine that no mtDNA introgression exists. Thus, the mtDNA was used to define a starting hypothesis for the clustering of specimens (Miralles and Vences, 2013). Species delimitation was then based on additional support from at least two of the following: (a) sympatric occurrence without admixture, as revealed by consistent differences in morphological or molecular characters at the same geographic location; (b) congruent diagnostic differences between sister lineages in morphological characters; and (c) the absence of haplotype sharing in nuclear loci. Integrative taxonomy therefore minimises the alpha error by only taking into account the most unambiguous species evidence provided by a variety of approaches and attempts to

keep the beta error low by seeking evidence from as many different approaches as possible (Miralles and Vences, 2013).

Results

Taxonomic implications of phylogenetic relationships

Results from the comprehensive molecular study (Melville et al., 2011) provide strong evidence that a taxonomic revision of *Lophognathus*, *Gowidon* and *Amphibolurus* is warranted (fig. 1). Within the clade containing *Amphibolurus*, *Chlamydosaurus* and *Lophognathus* (fig. 1), *Chlamydosaurus* forms a monophyletic group that is sister to the other genera. Based on these results, *Chlamydosaurus* is a well-supported genus. However, revision of *Amphibolurus* and *Lophognathus* is required. Molecular results show that *Amphibolurus*, for which *A. muricatus* is the type specimen, consists of *L. gilberti centralis*, *A. burnsi*, *A. muricatus* and *A. norrisi*. The genus *Lophognathus* contains only *L. gilberti*, but there is strong molecular evidence that *L. gilberti* is two species, a northern taxon and a more southern taxon (fig. 1). These two *L. gilberti* lineages are analysed further in the morphological section below, with the southern lineage referred to as *Lophognathus* sp. nov. Additionally, *Gowidon temporalis* and *G. longirostris*, which have previously been placed in *Lophognathus*, form two independent lineages that fall outside the *Amphibolurus*, *Chlamydosaurus* and *Lophognathus* clade. Based on these phylogenetic results, *G. temporalis* and *G. longirostris* should be placed in two separate genera. The name *Gowidon* (Wells and Wellington, 1984) has been used in recent publications (e.g. Wilson and Swan, 2017) based on molecular data (Melville et al., 2011). However, there is no available name for *G. temporalis* and a new genus is required (see taxonomic revision below). These generic designations are analysed further in the morphological section below.

Morphological analysis

Museum specimens for species in *Lophognathus*, *Gowidon* and *Amphibolurus* were analysed using ten morphometric characters and examined to identify morphological synapomorphies. Initially, the specimens that were sequenced in the molecular study (Melville et al., 2011) were examined to determine diagnostic characters for the six species identified in the phylogenetic analyses: *L. gilberti*, *L. sp. nov.*, *L. gilberti centralis*, *G. longirostris*, *G. temporalis* and *A. burnsi*. Once the diagnostic characters had been established, we then went through museum specimens (Supplementary Appendix S1) and primary types (Table 1) and assigned each of them to one of these species. All specimens were then measured and scored for morphometric and synapomorphic characters. A summary of morphometric characters for each species is presented in Table 2. While there is extensive variation within species in body colour, patterns and scalation, we were able to determine some consistent and diagnostic characters that differed between the taxa. These synapomorphies were particularly related to scalation and colour patterning on the head and upper body. These synapomorphies are covered in detail in the taxonomic revision section below.

Morphometric analyses – multivariate methods were used to examine the morphological differences between the six

Table 2. Mean morphological measurements (mm \pm standard error) for study species

Species	N	SVL	Tail	Hindlimb proximal	Hindlimb distal	Hindlimb autopod	Head length	Head depth	Head width	Femoral pores	Prealal pores
<i>Amphibolurus burnsi</i>	12	110.3 (± 4.69)	274.0 (± 13.45)	27.7 (± 1.29)	32.8 (± 1.42)	41.8 (± 1.23)	39.7 (± 1.67)	18.4 (± 1.60)	26.9 (± 1.82)	4 (3–5)	4 (4–6)
<i>Lophognathus gilberti centralis</i>	21	100.1 (± 3.62)	273.5 (± 10.36)	23.9 (± 0.92)	30.0 (± 1.15)	37.4 (± 0.91)	34.9 (± 1.38)	15.5 (± 0.81)	22.2 (± 1.47)	4 (2–6)	4 (3–6)
<i>Lophognathus gilberti gilberti</i>	25	86.8 (± 2.76)	246.9 (± 8.00)	21.6 (± 0.61)	27.1 (± 0.83)	36.0 (± 1.09)	30.2 (± 1.09)	13.6 (± 0.56)	18.7 (± 0.93)	4 (2–7)	4 (3–6)
<i>Lophognathus sp. nov.</i>	43	86.2 (± 2.73)	238.1 (± 9.26)	21.6 (± 0.63)	26.6 (± 0.76)	36.2 (± 0.92)	30.0 (± 1.14)	13.1 (± 0.51)	17.8 (± 0.84)	4 (2–8)	4 (3–6)
<i>Gowidon longirostris</i>	31	95.0 (± 1.48)	302.5 (± 5.7)	23.4 (± 0.47)	28.2 (± 0.52)	38.9 (± 0.65)	32.9 (± 0.81)	13.5 (± 0.39)	17.5 (± 0.56)	16 (11–22)	6 (4–7)
<i>Gowidon temporalis</i>	32	93.1 (± 2.33)	277.5 (± 6.56)	23.1 (± 0.56)	27.8 (± 0.78)	39.6 (± 0.76)	31.5 (± 0.98)	14.5 (± 0.52)	18.1 (± 0.93)	2 (1–6)	2 (1–3)

Note: SVL, snout–vent length.

Lophognathus species. We conducted a principal components analysis on the measured morphological characters (Table 3). Three morphological measurements were found not to vary significantly between species: proximal hindlimb; distal hindlimb and head length. Consequently, these characters were not included in the multivariate analyses.

Principal components analysis of the morphometric variables revealed that body proportions accounted for almost half of the variance in the data. This first principal component (PC1) explained 46.43% of the variance in morphology. Lizards scoring high on PC1 are large with relatively long hind feet, long tails, and deep or wide heads, while lizards scoring low on PC1 are small with short body proportions (Table 3). The second principal component (PC2) explained 19.69% of the variance in morphology. Lizards with high scores on PC2 had lower numbers of femoral and preanal pores, while lizards scoring low on PC2 had higher numbers of pores (Table 3). The third principal component (PC3) explained 14.40% of the variance in morphology. Lizards with high scores on PC3 had proportionally short hind feet, while lizards scoring low on PC3 had longer hind feet. Analysis of variance indicated a statistically significant difference between species on PC1 ($F_{5,136} = 12.61$, $P < 0.001$), and Tukey's honest significant difference *post hoc* test showed that *L. gilberti* and *L. sp. nov.* scored significantly lower on this principal component than *L. gilberti centralis* ($P = 0.029$ and $P = 0.003$, respectively), *A. burnsi* (both $P < 0.001$) and *G. longirostris* ($P = 0.039$ and $P = 0.010$, respectively) but not *G. temporalis*. In addition, *G. temporalis* had a significantly lower score than *G. longirostris* ($P < 0.001$) on PC1. Thus, relative to body size, *L. gilberti*, *L. sp. nov.* and *G. temporalis* have shorter or smaller body proportions than the other species.

Analysis of variance of PC2 also indicated a statistically significant difference between species ($F_{5,136} = 56.49$, $P < 0.001$). Tukey's honest significant difference *post hoc* test indicated that *G. temporalis* scored significantly higher on PC2 than all of the other taxa (all $P < 0.001$), indicating lower pore numbers, and *G. longirostris* scored significantly lower than all other taxa (all $P < 0.001$), indicating higher pore numbers. Analysis of variance of PC3 indicated a statistically significant difference between species ($F_{5,136} = 21.08$, $P < 0.001$) and Tukey's honest significant difference *post hoc* test indicated that on PC3, *G. temporalis* and *G. longirostris* scored significantly higher than all of the other taxa (all $P < 0.001$), indicating shorter hind feet length, relative to body size.

Although there is a statistically significant separation of these species in morphospace, it is visually difficult to ascertain (fig. 2). There is extensive overlap in morphospace, with *G. temporalis* and *G. longirostris* being the only species with visible separation from the others and that do not overlap each other in morphospace.

Species delimitation assessment

All available specimens were separated into groups based on the independent lineages supported in the mtDNA tree and then assessed for fixed and unambiguous morphological character states. We identified five morphologically diagnosable lineages that were also resolved as independent

Table 3. Principal components analysis of lizard morphology. Correlations with absolute values greater than 0.5 are in bold and are considered important.

	PC 1	PC 2	PC 3
% Variance explained	46.43	19.69	14.40
Eigenvalues	3.25	1.38	1.01
Component loadings			
SVL	0.81	0.37	−0.05
Tail	0.78	0.13	0.32
Hind foot	0.55	0.18	−0.77
Head width	0.80	0.10	0.27
Head depth	0.83	0.08	0.02
Femoral pores	0.40	−0.75	−0.42
Prealanal pores	0.45	−0.79	0.30
Species			
<i>Amphibolurus burnsi</i>	0.51 ± 0.34	0.65 ± 0.22	−0.71 ± 0.15
<i>Lophognathus gilberti centralis</i>	0.34 ± 0.24	0.44 ± 0.14	−1.09 ± 0.20
<i>Lophognathus gilberti gilberti</i>	−0.51 ± 0.16	0.10 ± 0.13	−0.29 ± 0.20
<i>Lophognathus</i> sp. nov.	−0.54 ± 0.17	−0.12 ± 0.10	−0.24 ± 0.14
<i>Gowidon longirostris</i>	0.85 ± 0.10	−1.32 ± 0.10	0.65 ± 0.12
<i>Gowidon temporalis</i>	−0.28 ± 0.13	1.13 ± 0.13	0.83 ± 0.14

Note: PC, principal component; SVL, snout–vent length.

lineages in the mtDNA and nuclear trees, which were equated to generic level divisions (fig. 3). Within lineages, further morphologically diagnosable lineages, which were also well-supported in the mtDNA and nuclear trees, could be identified. A number of these lineages have wholly or partially overlapping geographic distributions within the Australian tropical savannah (fig. 4): *Lophognathus gilberti gilberti*, *L. gilberti centralis*, *L. gilberti* sp. nov. and *Chlamydosaurus kingi*. Using this species delimitation method, five genera and nine species could be delineated across *Amphibolurus*, *Gowidon* and *Lophognathus* sensu lato.

Taxonomic revision

Diagnoses below are given only in terms of synapomorphies. Species diagnoses are only provided for those species for which taxonomic revision is required.

Genus *Amphibolurus* Wagler, 1830

Gemmatophora Kaup, J.J., 1827. Zoologische Monographien. *Isis Von Oken*, Jena 20: 610–625 [621] [*nom. oblit.*; described as subgenus of *Calotes* Cuvier, 1817]. Type-species *Lacerta muricata* White, 1790 by original designation.

Amphibolurus Wagler, J.G., 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel*. München, Cotta'schen vi 354 pp. [145] [replacement for *Gemmatophora* Kaup, 1827, which Wagler rejected as an invalid

hybrid name (“vox hybrida”)].

Grammatophora Duméril, A.M.C. and Bibron, G., 1837. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Paris, Roret 4: ii 571 pp. [468] [*non Grammatophora* Stephens, 1829 (*nom. nud.*); emendation of *Gemmatophora* Kaup, 1827].

Petroplanis Fitzinger, L.J., 1843. *Systema Reptilium*. Vienna, Braumüller u. Seidel vi 106 pp. [83, 84] [*nom. nud.*; introduced in synonymy of *Amphibolurus* Wagler, 1830]. Types species *Petroplanis jacksoniensis* Fitzinger, 1843 (= ? *Agama jacksoniensis* Cloquet, 1816) by monotypy.

Polylophus Fitzinger, L.J., 1843. *Systema Reptilium*. Vienna, Braumüller u. Seidel vi 106 pp. [83, 84] [*nom. nud.*; introduced in synonymy of *Amphibolurus* Wagler, 1830]. Types species *Polylophus jacksoniensis* Fitzinger, 1843 (= ? *Agama jacksoniensis* Cloquet, 1816) by monotypy.

Synonymy that of: Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. *Amphibia and reptiles*. Pp. 108–116 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [108]

Diagnosis. A genus consisting of large agamid lizards in the subfamily Amphibolurinae with exposed tympanum, long robust limbs and a long tail. Gular scales smooth to weakly keeled, ventral scales smooth to strongly keeled. Head wide and deep in comparison with length. Heterogenous body scales, dorsal surface scattered with many spinose scales. Well-developed spinose nuchal and vertebral crest. Two broad pale dorsolateral stripes running from ear or neck to the hip,

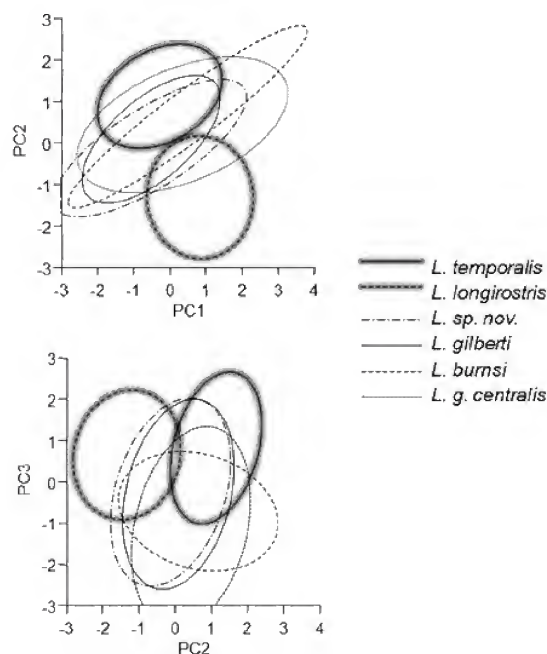


Figure 2. The distribution of *Lophognathus* sensu lato samples included in this study along the first three morphological principal components axes. Distribution of each taxon is delineated by a 95% confidence ellipse. *Lophognathus gilberti* has been separated into *L. sp. nov.*, *L. gilberti centralis*, and *L. gilberti*.

discontinuous with pale lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length.

Included species. *Amphibolurus norrisi* Witten, G.J. and Coventry, A.J., 1984; *Lacerta muricata* White, J., 1790; *Amphibolurus burnsi* Wells, R.W. and Wellington, C.R., 1985; *Physignathus gilberti centralis* Loveridge, A., 1933.

Distribution. Continental Australia, including south-eastern Australia extending west across Nullabor Plain, eastern Australia extending north into Queensland, central Australia incorporating Northern Territory, Western Australia and western Queensland. A broad range of habitats occupied, including arid and semi-arid woodlands, dry sclerophyll forests and woodlands, and coastal heathlands.

Amphibolurus burnsi

(fig. 8)

Amphibolurus burnsi Wells, R.W. and Wellington, C.R., 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplementary Series* 1: 1–61 [18]. Designation that of Melville, J., this work.

Holotype. AM R116981 (previously AMF 28917), Collarenebri, New South Wales.

Diagnosis. Large robust member of the *Amphibolurus* genus. Large wide head with extensive covering of spinose scales. Posterior ventral portion of head heavily covered with spinose scales. Well-developed spinose nuchal and vertebral crest, which continues down back to hips. At least two more spinose dorsal crests on each side of vertebral crest. Scalation on back strongly heterogeneous, with two dorsolateral rows of spinose scales running from shoulders to hips. Scales on thighs strongly heterogeneous with scattered spinose scales. Prominent row of spinose scales running along the posterior edge of thighs. Shades of brown, grey to almost black. Two broad pale dorsolateral stripes running from ear or neck to the hip, discontinuous with lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length. Femoral pores 3–5; preanal pores 4–6.

Description of holotype. Adult. Large robust lizard with distinct neck, limbs long and robust; canthus well defined; nasal scale below canthal ridge, nare slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 12; supralabials 13. Labials elongate somewhat keeled. Scales on dorsal surface of head heterogeneous and strongly keeled. Well-developed spinose nuchal crest. Posterior portion of head heavily covered with spinose scales. Well-developed vertebral crest, which continues down back to hips. Two paravertebral rows of enlarged and prominent spinose scales on each side of vertebral crest, running from shoulders to hips. Scales on thighs strongly heterogeneous with scattered spinose scales. Row of enlarged spinose scales running along posterior edge of thighs. Scales on the dorsal surface of body and tail are strongly keeled and scales on the ventral surface are weakly keeled. Colour dorsally is light to dark brown and grey, with scattered black markings.

Variation. Considerable variation in the number and size of spinose scales between males, females and juveniles. In adult males there are numerous long spines (> 2 mm) and the spinose scales are dense across the back of the head, nuchal and ventral crests, and rear of the thighs. In females and juveniles, spinose scales are still present and diagnostic but they are smaller and less dense, providing an overall appearance of the lizards being less spiny. Some individuals, particularly adult males, have a broad pale stripe running along the full extent of the lower lip. However, a white stripe along the upper lip is not present and a well-defined pale stripe between the eyes and ears is not present.

Distribution and ecology. Occurs in dry woodlands and associated with eucalypts along inland watercourses. Distributed across southern and central-western Queensland and northern inland New South Wales.

Remarks. The distribution of *Amphibolurus burnsi* potentially overlaps with *A. centralis* and *A. muricatus*. *A. burnsi* has been included in the genus *Lophognathus* but DNA sequencing has confirmed that it is unrelated to *Lophognathus* species and demonstrates a clear sister-species relationship with *A. centralis*. Morphologically, *A. centralis* and *A. burnsi* can be distinguished by the latter having heterogeneous scales on the thighs, spinous scales on the thigh and enlarged spinous scales along the rear of the thigh.

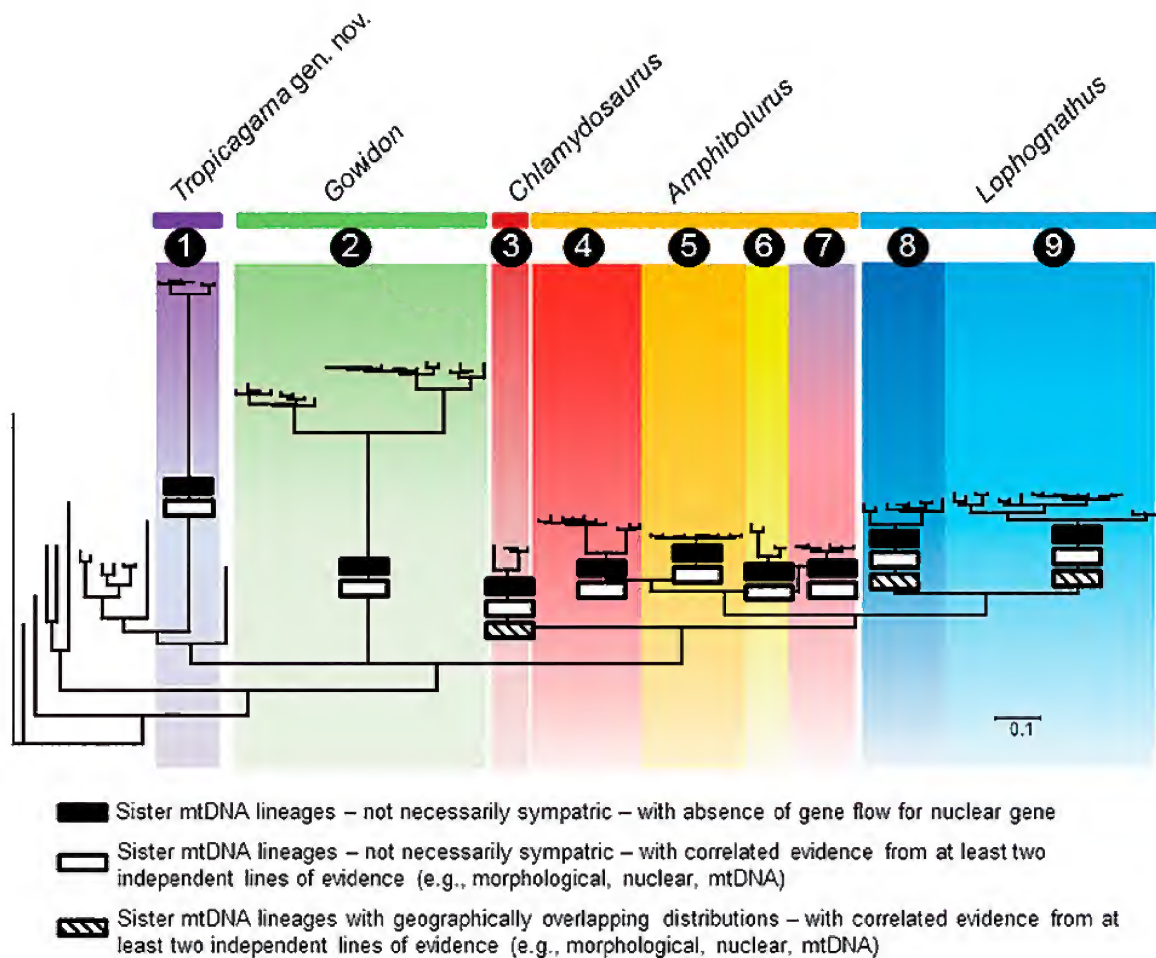


Figure 3. Results from the integrative taxonomic approach to species delimitation. Genera are designated by a multicoloured horizontal bars at the top of the figure, and species within genera are designated by a number in black above a coloured vertical segment. Segment colours and species numbers correspond to those in fig.1.

Amphibolurus centralis

(Figs. 5 & 8)

Physignathus gilberti centralis Loveridge, A. 1933. New agamid lizards of the genera *Amphibolurus* and *Physignathus* from Australia. *Proceedings of the New England Zoological Club*, Boston 13: 69–72 [71]. Designation that of Wells, R.W. and Wellington, C.R., 1983. A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* 1: 73–129 [80].

Holotype. MCZ 35207, Anningie 30 mi[les] W of Teatree Well, Northern Territory.

Paratype. AM R10993 (formerly MCZ 35208), Australia, Northern Territory, Tea Tree Well, (22° 8' S, 133° 24' E). Juvenile. Note: Original MCZ catalogue lists locality information identical to MCZ 35207.

Diagnosis. Large robust member of the *Amphibolurus* genus. Large wide head in proportion to body size. Well-developed spinose nuchal and vertebral crest. Scalation on back heterogeneous. Scales on thighs relatively homogeneous, lacking row of large spinose scales. Shades of light to dark brown and grey. Two broad pale dorsolateral stripes running from ear or neck to hip, discontinuous with pale lip scales. Dorsolateral stripes intersected by multiple wedges of brown or grey along their length. Most individuals have a broad pale or white stripe running along extent of the lower lip. Femoral pores 2–6; preanal pores 3–6.

Description of holotype. Adult male. Large robust lizard with large wide head in proportion to body size and well-developed spinose nuchal crest comprising a row of eight enlarged scales.

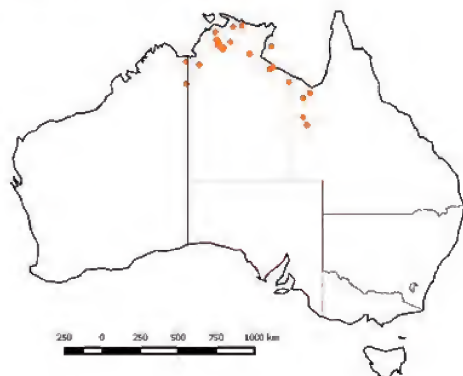
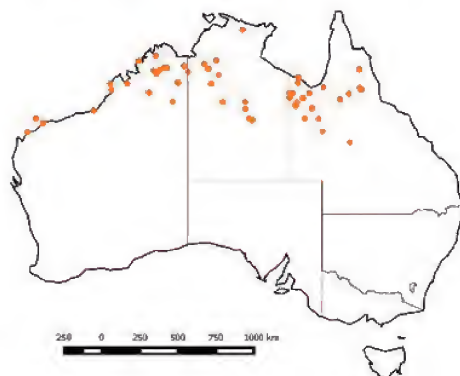
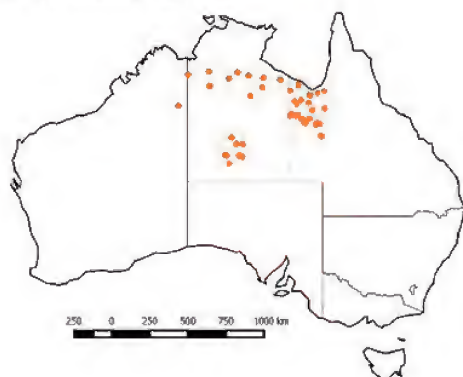
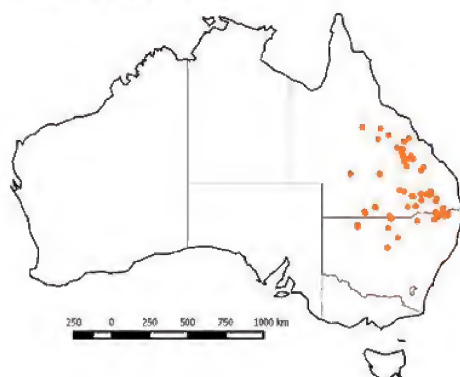
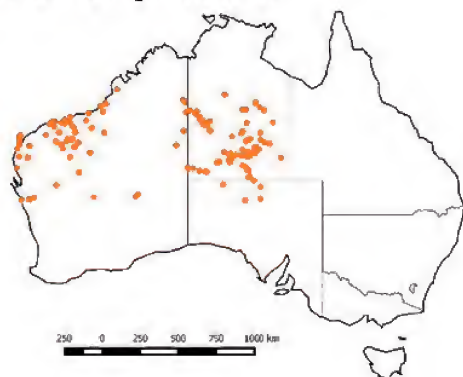
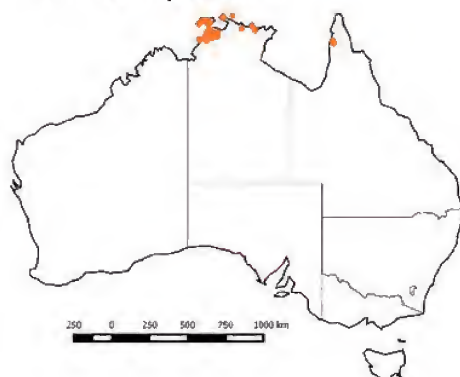
a. *L. gilberti*b. *L. horneri* sp. nov.c. *A. centralis*d. *A. burnsi*e. *G. longirostris*f. *T. temporalis*

Figure 4. Distribution of study species included in this study, compiled from museum records.

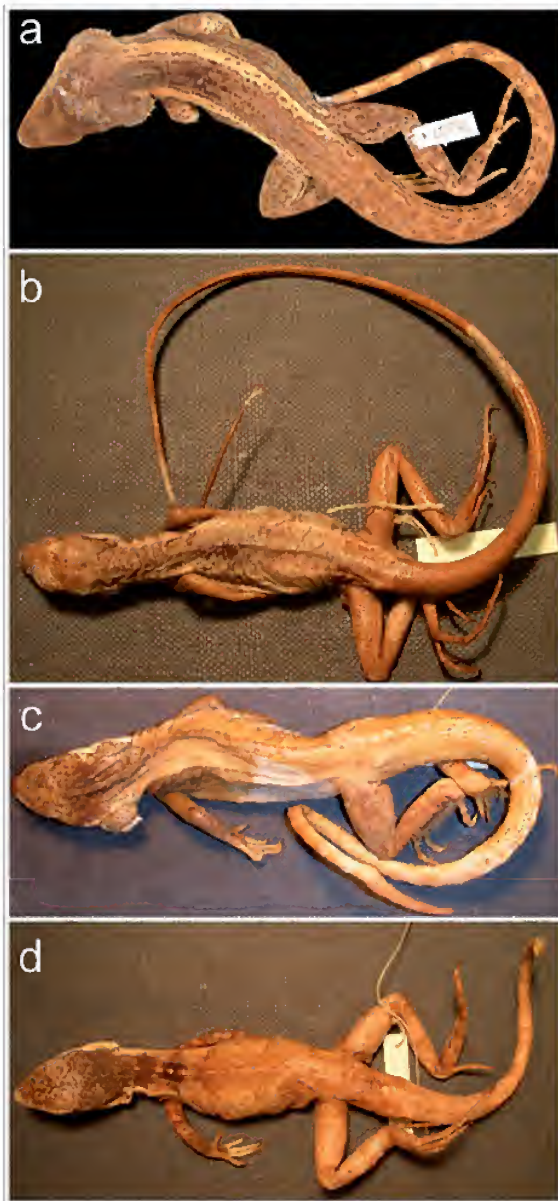


Figure 5. Primary type specimens: a, *Amphibolurus centralis* (MCZ 35207); b, *Gowidon longirostris* (BMNH 1946.8.28.73); c, *Lophognathus gilberti* (BMNH 1946.8.28.69); d, *Tropicagama temporalis* (BMNH 1946.8.28.72).

Additional (4–6) enlarged spinose scale protruding from rear of head, posterior to the jaw. Scales on thighs relatively homogeneous, lacking row of large spinose scales. Distinct neck, limbs long and robust; canthus well defined; nasal scale below canthal ridge, nares slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 13,

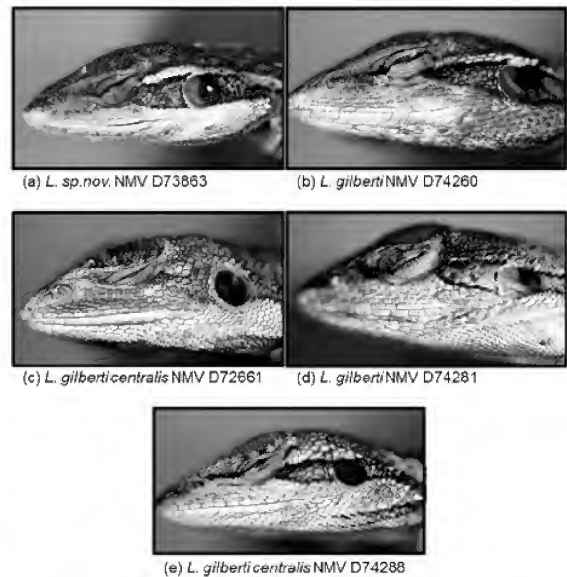


Figure 6. Colour pattern variation in the lateral head views of *Amphobolurus centralis*, *Lophognathus gilberti* and *L. horneri* sp. nov. Museum registration numbers for the individual lizards photographed are provided.

supralabials 14. Labials elongate without obvious keels. Scales on dorsal surface of head heterogeneous and strongly keeled. Scattered enlarged, keeled mucronate scales present on side of head posterior to the eye. Scales on the dorsal surface of body and tail are strongly keeled and scales on the ventral surface are weakly keeled. Tail long, robust at base, tapering distinctly from approximately one-third along its length to a fine tip. Shades of cream, light to dark brown and grey. Two broad pale dorsolateral stripes running from rear of head to back of rear legs; pale stripes bordered by narrow discontinuous dark brown stripes along entire length and flecks of dark brown within the posterior two-thirds of the pale stripes. Irregular dark brown colouration between the pale dorsolateral stripes on the anterior one-third of the torso. Lacking pale stripe running along the extent of the lower lip.

Variation. Marked variation in colour pattern between individuals. Broad white lip stripe occurs along the upper lip in some individuals, mostly adult males. Alternatively, some individuals do not have a white stripe on either the upper or the lower lips. Diffuse pale stripe between eye and ear in some individuals, but it is not a well-defined stripe bordered dorsally and ventrally by a row of darker scales extending the full span of eye–ear.

Distribution and ecology. Arid northern-central and central Australia, particularly associated with mulga woodlands but also occurring in eucalypt woodlands. Western Queensland, Northern Territory and Western Australia.

Table 4. Summary of morphometric measurements (mm) for the primary types of *Amphibolurus burnsi*, *A. centralis*, *Gowidon longirostris*, *Lophognathus gilberti*, *L. horneri* sp. nov. and *Tropicagama temporalis*

	<i>Amphibolurus burnsi</i>	<i>Amphibolurus centralis</i>	<i>Gowidon longirostris</i>	<i>Lophognathus gilberti</i>	<i>Lophognathus horneri</i> sp. nov.	<i>Tropicagama temporalis</i>
	AM R116981 Holotype	MCZ 35207 Holotype	BMNH 1946.8.28.73 Lectotype	BMNH 1946.8.28.69 Holotype	NTM R16472 Holotype	BMNH 1946.8.28.72 Lectotype
SVL	105.2	99.6	88.8	112.9	102	102.7
HL	39.4	38.3	29.1	40.2	36.1	31.3
HW	31.0	29.6	18.9	27.5	23.2	19.5
HD	13.3	12.2	12.8	14.5	14.4	13.2
LegL	88.6	85.2	83.9	105.6	102.0	87.1

Note: SVL, snout–vent length; HL, head length; HW, head width at widest point; HD, head depth; LegL, hindlimb length.

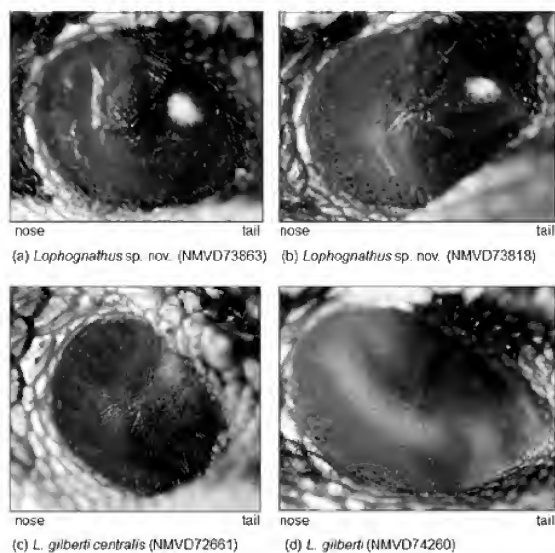


Figure 7. Variation in white pigmentation on tympanums of *Lophognathus* sp. nov., *L. gilberti* and *L. gilberti centralis*. Orientation of the tympanums is provided under images. Museum registration numbers for the individual lizards photographed are also provided.

Remarks. As detailed above, the distribution of *Amphibolurus centralis* potentially overlaps with *A. burnsi* Wells and Wellington, 1985, *Gowidon longirostris* Boulenger, 1883, *Lophognathus gilberti* Gray, 1842 and *L. horneri* sp. nov. DNA sequencing has confirmed that *Amphibolurus centralis* is unrelated to the *Gowidon* and *Lophognathus* species and demonstrates a clear sister-species relationship with *A. burnsi*. Morphologically, *A. centralis* can be distinguished from *A. burnsi* by having mostly homogeneous scales on the thighs,

lacking spinous scales on the thigh and having no enlarged spinous scales along the rear of the thigh.

Genus *Gowidon* Wells and Wellington, 1984.

Gowidon Wells, R.W. and Wellington, C.R., 1983. A synopsis of the Class Reptilia in Australia. *Australian Journal of Herpetology* 1: 73–129. Type-species *Gowidon longirostris* Boulenger, G.A., 1883 by monotypy.

Diagnosis. A monotypic genus consisting of a large agamid lizard in the subfamily Amphibolurinae with exposed tympanum, gular scales smooth to weakly keeled, ventral scales smooth to weakly keeled. Long-limbed, very long tail, long snout and distinct nuchal crest. Head narrow and shallow in depth compared with length of snout. Dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes and pale stripe along lower jaw. One to three small white spots on a black background positioned directly posterior to the ear. Preanal pores 4–7; femoral pores range 11–22.

Included species. *Gowidon longirostris* Boulenger, G.A., 1883.

Distribution. Arid western interior of Australia. Semi-arboreal, occurring in a broad range of habitats across arid and semi-arid habitats, particularly associated with inland arid watercourses, gorges and river beds.

Gowidon longirostris

(Figs. 5 & 8)

Gowidon longirostris Boulenger, G.A., 1883. Remarks of the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 12(5): 225–226 [225].

Physignathus eraduensis Werner, F., 1909. Reptilia exkl. Geckonidae and Scincidae. In Michaelsen, W. and Hartmeyer, R. (eds.) *Die fauna südwest-Australiens*. Jena: Gustav Fischer 2: 251–278 [275]. Type data. holotype, status unknown, from Eradu, Western Australia.

Physignathus longirostris quattuorasciatus Sternfeld, R., 1924. Beiträge zur herpetology inner-Australiens. *Abhandlungen der*



Figure 8. Photos in life of species under revision: a, *Lophognathus horneri* sp. nov., adult male with breeding colouration, 80 mile beach, Western Australia (photo: R. Glor); b, *Lophognathus gilberti*, Katherine, Northern Territory (photo: R. Glor); c, *Amphibolurus centralis*, adult male with breeding colouration, West MacDonnell Ranges, Northern Territory (photo: J. Melville); d, *Amphibolurus burnsi*, adult male with breeding colouration, Westmar, Queensland (photo: S. Wilson); e, *Tropicagama temporalis*, Jabiru, Northern Territory (photo: S. Wilson); f, *Gowidon longirostris*, adult male with breeding colouration, Ormiston Gorge, Northern Territory (photo: R. Glor).

Senckenbergischen Naturforschenden Gesellschaft 38: 221–251 [236]. Type data. lectotype SMF 10366, from Hermannsburg Mission, Northern Territory. Designation by Mertens, R., 1967. Die Herpetologische Section des Natur-Museums und Forschungs-Institutes Senckenberg in Frankfurt-a-M. nebst einem Verzeichnis ihrer Typen. 1. *Senckenberg Biology* 48: 1–106.

Synonymy that of: Melville, J., this work; Cogger, H.G., 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].

Lectotype. BMNH 1946.8.28.73, Champion Bay, Western Australia. Designation by Wells, R.W. and Wellington, C.R., 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology Supplementary Series* 1: 1–61. Paralectotypes BMNH 1946.8.12.64–65, Nickol Bay, Western Australia.

Diagnosis. As for genus.

Description of Lectotype. Adult. Moderately sized slender agamid lizard with relatively long snout and dorsoventrally compressed head. A distinct neck, very long limbs and very long whip-like tail; canthus well defined; nasal scale below canthal ridge, nares slightly to the posterior–dorsal section of the nasal scale; visible tympanum. Infralabials 13; supralabials 15. Labials elongate unkeeled. Scales on dorsal surface of head moderately heterogeneous and weakly to moderately keeled. Low nuchal crest of slightly enlarged scales, extending as a row of enlarged vertebral scales down the back to base of tail. Lacking enlarged spinose scales on head or torso. Dorsal scales on body and tail mostly homogeneous and moderately keeled. Scales on thighs homogeneous and strongly keeled. Scales on ventral surface of head strongly keeled and weakly keeled on the body. Colour dorsally is light to dark brown and grey. Broad white lip stripe, widest on lower jaw and narrow on upper lip, extends below ear and as two broad white dorsoventral stripes extending to mid-way down the back. A dark diffuse area of pigmentation behind ear with diffuse pale spot immediately behind the tympanum but the characteristic well-defined white spot or spots on a black background behind the ear is not apparent. Ventral surface of head, throat and upper chest darkly pigmented with the dark pigmentation extending to the lateral surfaces of the throat and up over the shoulders, bordering the white dorsolateral stripes.

Variation. A few specimens examined lack the broad dorsolateral stripes and are a pale grey colour, with a few rust-brown coloured markings between the shoulders. An example of this colour-morph is NMVD74317 collected on the Great Northern Highway, 1 km E of Roebuck Roadhouse, Western Australia (17° 48' 57"S, 122° 40' 44" E). However, these pale colour morphs still retain the white spot or spots on a black background behind the ear.

Distribution and ecology. Arid western interior of Australia. Semi-arboreal, occurring in a broad range of habitats across arid and semi-arid habitats, particularly associated with inland arid watercourses, gorges and river beds.

Remarks. The distribution of *Gowidon longirostris* overlaps with *Amphibolurus centralis* and *Lophognathus horneri* sp. nov. but can be distinguished morphologically by having more

than 10 femoral pores, ≥ 1 white spot on a black background behind the ear, a relatively long snout and dorsoventrally compressed head, and a very long whip-like tail.

Genus *Lophognathus* Gray, 1842

Lophognathus Gray, J.E., 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany*. London: Treuttel, Würz & Co. [53]. Type-species *Lophognathus gilberti* Gray, 1842 by monotypy.

Redtenbacheria Steindachner, F., 1867. *Redtenbacheria fasciata* Steindachner, F., 1867. Reptilien. Pp. 1–98 in: *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Willerstorff-Urbair*. Zoologie 1(3). Vienna: State Printer. [1869 on title page] [31]. [junior homonym of *Redtenbacheria* Schiner, 1861]. Type species. *Redtenbacheria fasciata* Steindachner, 1867 by monotypy.

Synonymy that of: Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [121]

Diagnosis. A genus consisting of large agamid lizards in the subfamily Amphibolurinae, with exposed tympanum, gular scales smooth to weakly keeled, ventral scales weakly to strongly keeled. Stoutly built with moderately long legs and tail. Broad white stripe on the upper and lower lips, extending along the full extent of the jaw, pale stripe from behind the eye to the top of the ear, which is cream, white, grey or yellow in life. This pale stripe is well defined ventrally and dorsally by a row of darkly pigmented scales (fig. 6). Heterogenous scales on the back both at the midline and dorso-laterally, associated with a weak to prominent row of enlarged, strongly keeled scales. Colour patterns of grey, brown, rust-brown and black. Well-developed nuchal crest continuous with the enlarged row of vertebral scales. Broad pale dorsolateral stripes, which may extend from top of ear or back of head to hips. Dorsolateral stripes are not continuous with the pale lip stripes. On the back, dorsolateral stripes may be intersected by wedges of brown or grey. Preanal pores 3–6; femoral pores 2–8.

Included species. *Lophognathus gilberti* Gray, J.E., 1842; *Lophognathus horneri* sp. nov.

Distribution. Northern Australia, extending from northern-central and western Queensland, through the northern regions of the Northern Territory and across northern Western Australia. Occurs in woodlands and river courses.

Lophognathus gilberti

(fig. 5)

Lophognathus gilberti Gray, J.E., 1842. Description of some hitherto unrecorded species of Australian reptiles and batrachians. Pp. 51–57 in: Gray, J.E. (ed.). *The zoological miscellany*. London: Treuttel, Würz & Co. [53].

Redtenbacheria fasciata Steindachner, F. 1867. Reptilien. Pp. 1–98 in: *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Willerstorff-Urbair*. Zoologie 1(3). Vienna: State Printer. [1869 on title page] [31]. Type data. Holotype whereabouts unknown (not found), Australia.

Physignathus incognitus Ahl, E. 1926. Neue Eidechsen und Amphibien. *Zoologischer Anzeiger* 67: 186-192 [190]. Type data. Holotype ZMB 30086, Australia.

Synonymy that of: Melville, J., this work; Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. Amphibia and Reptiles. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [121].

Holotype. BMNH 1946.8.28.69 from Port Essington, NT.

Diagnosis. As for genus. *Lophognathus gilberti* is distinguished from *Lophognathus horneri* sp. nov. by lacking a distinct white spot on the tympanum (fig. 7) that is surrounded by or adjacent to black pigmentation.

Description of Holotype. A large robust male dragon lizard with large robust limbs and tail. Large head in comparison with body size, prominent nuchal crest of 18 enlarged spinose scales, extending from anterior of ear to shoulders. Small nasal scale and nares, below canthal ridge. Supralabials 13; anterior point of lower jaw damaged. Head scales heterogeneous and strongly keeled; 3–5 enlarged white spinose scales protruding from rear of head, posterior to the jaw. Dorsal scales on body and tail strongly keeled and heterogeneous. Gulars smooth and ventrals weakly to strongly keeled. Scales on thighs heterogeneous and strongly keeled. Very broad white lip stripes, extending under jaw and up to anterior border of ear. Broad pale dorsolateral stripes, continuous from neck to hips, bordered and well defined by row of darker scales. Dorsolateral stripes discontinuous with lip stripes. Poorly defined and discontinuous pale stripe between eye and top of ear, bordered dorsally and ventrally by darker scales. No clearly defined white spot on a dark background on the tympanum, although there is a patch of pale pigment in the upper-back quadrant of the tympanum. Colour dorsally is light to dark brown and grey. Ventral surface of head, throat and upper chest darkly pigmented with the dark pigmentation extending to the lateral surfaces of the throat and up over the shoulders, bordering the white dorsolateral stripes. Femoral pores 6; preanal pores 4.

Variation. Some specimens of *L. gilberti* do have white areas on the tympanum but they are not a well-defined spot surrounded by the black pigmented area (fig. 7); instead, they are a diffuse white or off-white smear or patch of pale pigment without the associated black pigmentation. An example of this is specimen NMVD74026 collected from Mt Wells Road, near Grove Hill in the Northern Territory (13° 28' 47" S, 13° 132' 41" E), which has a smear of white pigmentation across the posterior half of the tympanum.

Distribution and ecology. Far northern Australia in woodlands and tropical savannahs. In the Northern Territory north of Katherine, in Arnhem Land, and across coastal areas into Western Australia and western Queensland. In Western Australia, occurs north of Kununurra and extending up into the eastern coastal Kimberley.

Remarks. *Lophognathus gilberti* shares similar body proportions and meristic characters with *L. horneri* sp. nov., with extensive distributional overlap (fig. 4) but is readily separated by the lack of a well-defined white spot on the tympanum. *Lophognathus gilberti* is also superficially similar

to *Amphibolurus centralis* and potentially has distributional overlap, but it differs in mostly having a well-defined white or pale stripe extending the full length between the ear and the eye, and a broad white stripe running the extent of the upper lip being mostly present.

Lophognathus horneri sp. nov.

ZooBank LSID: urn:lsid:zoobank.org:act: 4E027CDD-F9B2-451B-B08E-26D6A0B8A8ED.

(Figs. 8 & 9)

Grammatophora temporalis (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45–68 [52].

Synonymy that of: Melville, J., this work.

Holotype. NTM R16472 Sambo Bore, Wave Hill Station, Northern Territory (18° 52' 48" S, 130° 40' 12" E).

Paratypes. NMV D72658 Wave Hill Homestead, Northern Territory (17° 23' 08" S, 131° 06' 44" E); NMV D73846 King Edward River Camp, Mitchell Plateau, Kimberley, Western Australia (14° 52' 57" S, 126° 12' 10" E); NMV D74687 road to Davenport Ranges National Park, Northern Territory (20° 37' 34" S, 134° 47' 14" E); WAM R131990 Kununurra, Kimberley, NE Western Australia (15° 48' 0.00" S, 128° 43' 0.12" E); WAM R108806 Mabel Downs Station, Calico Springs, NE Western Australia (17° 16' 59.88" S, 128° 10' 59.88" E); WAM R132850 Kununurra, NE Western Australia (5° 47' 37.68" S, 128° 43' 10.92" E); BMNH 1946.8.12.73 Nickol Bay, Western Australia [paralectotype *Grammatophora temporalis* (part.) Günther, 1867].

Diagnosis. A member of the Australian genus *Lophognathus* Gray, 1842, characterised by broad white stripe on the upper and lower lips, extending along the full extent of the jaw, a pale stripe from behind the eye to the top of the ear, which is cream, white, grey or yellow in life. This pale stripe is well defined ventrally and dorsally by a row of darkly pigmented scales (fig. 6). It is a large robust dragon with long head and well-built moderately long limbs. It has heterogenous scales on the back, both at the midline and dorsolaterally, associated with a weak to prominent row of enlarged strongly keeled scales. *Lophognathus horneri* is distinguished from *Lophognathus gilberti* by the presence of a distinct white spot on the tympanum (fig. 7). This well-defined white spot is wholly surrounded or bordered dorsally and to the anterior by an area of black pigmentation that is positioned on the upper posterior quarter of the tympanum. This area of black pigmentation also runs along a raised ridge that extends from the outer dorsoposterior edge of the tympanum towards its centre (fig. 9).

Description of holotype. A large robust male dragon lizard (snout–vent length: 102 mm; head length: 36.1 mm; head width at widest point: 23.2 mm; head depth: 14.4 mm; hindlimb length: 102 mm). Head moderately long and wide, slightly rounded profile of snout and slightly dorsolaterally compressed. Nuchal crest low, extending from anterior of ear to shoulders and composed of enlarged strongly keeled scales. Gulars smooth and ventrals weakly to strongly keeled. Dorsal scales strongly keeled and heterogeneous in size. Broad pale dorsolateral stripes, continuous from neck to the hips, bordered and well-defined by row of darker scales. Dorsolateral stripes discontinuous with lip stripes. Well-defined pale stripe between eye and top of ear,



Figure 9. Holotype of *Lophognathus horneri* sp. nov. (NTM R16472).

bordered dorsally and ventrally by row of darker scales. Well-defined white spot on the tympanum, which is adjacent to an area of black pigmentation that runs along a raised ridge that extends from the outer dorsoposterior edge of the tympanum towards its centre. Femoral pores 2L/3R; preanal pores 4.

Variation. The white stripe on the lower lip and the white spot on the tympanum are always present. The white stripe between the eye and the ear is almost always present. The broad white stripe on the upper lip can be pale and not prominent in a few individuals. The pale dorsolateral stripes are not continuous

with the white lip stripes. Dorsolateral stripes are often absent between the ear and neck or are intersected by wedges of darker scales along the back. Three specimens collected from 80 Mile Beach (fig. 8), Western Australia (NMV D74362–D74364), lacked a distinct stripe between the eye and the ear – superficially similar to *Amphibolurus centralis* – but they still had the white spot on the tympanum. A range of specimens were examined from large adult males, females, juveniles and hatchlings. All these specimens had a white stripe on the lower lip and the white spot on the tympanum.

Coloration in alcohol. Specimens retain key diagnostic characters in preservative. For example, the paralectotype *Grammatophora temporalis* (part.) BMNH 1946.8.12.73 from Nickol Bay, Western Australia, which has also been designated as a paratype for *L. horneri* sp. nov., was collected before 1867. This specimen, which has been in preservative for over 150 years, still retains diagnostic characters: broad white stripe on upper and lower lips, white spot on the tympanum and a pale stripe between eye and ear, which is bordered ventrally and dorsally by a row of darkly pigmented scales.

Distribution and ecology. Arid and semi-arid eucalypt woodlands and tropical savannahs of the central and western portions of northern Australia. Specimens were collected in 2009 as far south as the Davenport Ranges in the Northern Territory, which are south-east of Tennant Creek. This species extends north of Threeways but south of Katherine, west through Timber Creek and Wave Hill and into Western Australia. They have been collected in the Kununurra area, along the Gibb River Rd and in the Mitchell Plateau area. In Western Australia they extend south of Halls Creek and down to the northern Pilbara coast, south-west to Coral Bay and offshore islands.

Comparison with other species. *Lophognathus horneri* shares similar body proportions and meristic characters with *L. gilberti* with extensive overlap (Tables 2 and 3; fig. 4). It is readily separated from this species by the presence of a well-defined white spot on the tympanum (fig. 7), which is wholly surrounded or bordered by an area of black pigmentation. *Lophognathus horneri* is also superficially similar to *Amphibolurus centralis*, but it differs in having proportionally shorter tail, hindlimbs and head. Additionally, *L. horneri* has a well-defined white spot on the tympanum and a well-defined stripe between the eye and the ear (figs 6 and 7), which are lacking in *A. centralis*. Some specimens of *L. gilberti* and *A. centralis* do have white areas on the tympanum but they are not a well-defined spot surrounded or adjoining the black pigmented area; instead, they are a diffuse white or off-white smear or a patch of pale pigment without the associated black pigmentation. *Lophognathus horneri* can be distinguished from *Tropicagama temporalis* gen. nov. by having a well-defined stripe between the eye and the ear and heterogeneous dorsolateral scales along the back. In addition, *Lophognathus* has > 2 preanal pores, whereas *Tropicagama temporalis* gen. nov. has only two. *Gowidon longirostris* differs from *L. horneri* by having very long limbs and tail, being dorsoventrally compressed, having 1–3 white spots on a black background behind the ear and having > 10 femoral pores.

Etymology. This species is named in honour of Paul Horner, the Curator of Terrestrial Vertebrates at the Museum and Art Gallery of the Northern Territory, in recognition of his contributions to the knowledge of the tropical lizard fauna of Australia and his instrumental role in the taxonomic review of agamid lizards from this region.

Genus *Tropicagama* gen. nov.

ZooBank LSID: urn:lsid:zoobank.org:act: F534B4D5-CBD7-41E0-950A-B95B14F1D858.

Type-species. *Grammatophora temporalis* (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45–68 [52] [one of the original syntype series, BMNH 1946.8.12.73 (Nickol Bay), represents *Lophognathus horneri* sp. nov.].

Diagnosis. A monotypic genus consisting of a large agamid lizard in the subfamily Amphibolurinae, with exposed tympanum, gular scales smooth to weakly keeled, ventral scales smooth to weakly keeled. Very long-limbed, prominent erectable nuchal crest. Long tail and head relatively narrow for length. Dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes that are broadly continuous with wide pale stripe along upper and lower jaw. Lacks well-defined pale stripe between eye and ear. Upper portion of head usually dark grey or black and uniformly coloured. Under the head, on the chin, gular and neck areas, there is dark grey or black uniform pigmentation in adult males, with two narrow white stripes extending from the back of the jaw anteriorly under the chin, parallel to the jaw, ending approximately half way along the jaw. Femoral pores 1–6; preanal pores 2 (range 1–3).

Included species. *Grammatophora temporalis* (part.) Günther, A., 1867.

Distribution. Far northern Australian coastal regions in the Northern Territory and western Cape York. Also occurs on northern offshore islands, including Indonesian islands close to Australian waters and southern Papua New Guinea.

Tropicagama temporalis

(Figs. 5 & 8)

Grammatophora temporalis (part.) Günther, A., 1867. Additions to the knowledge of Australian reptiles and fishes. *Annals and Magazine of Natural History* 20(3): 45–68 [52] [one of the original syntype series, BMNH 1946.8.12.73 (Nickol Bay), represents *Lophognathus horneri* sp. nov.].

Lophognathus lateralis Macleay, W., 1877. The lizards of the Chevert Expedition. Second paper. *Proceedings of the Linnean Society of New South Wales* 2: 97–104 [1878 on title page] [103]. Type data. Holotype AM R31882, Mawatta, Binaturi River (as Katow), Papua New Guinea.

Lophognathus labialis Boulenger, G. A., 1883. Remarks on the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 5 12: 225–226 [225]. Type data. Syntype(s) BMNH 1946.8.12.72, Port Essington, NT; BMNH 1946.8.12.63.

Lophognathus maculilabris Boulenger, G. A., 1883. Remarks on the lizards of the genus *Lophognathus*. *Annals and Magazine of Natural History* 12(5): 225–226 [226]. Type data. Syntypes: BMNH 1946.8.28.70–71 (BMNH 1919.8.26.13–14), Timor Laut Islands, Indonesia.

Synonymy that of: Melville, J., this work; Cogger, H.G. 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. *Amphibia and Reptiles*. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1. Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].

Lectotype. BMNH 1946.8.28.72, Port Essington, Northern Territory. Designation by Cogger, H.G., 1983, in Cogger, H.G., Cameron, E.E., and Cogger, H.M. *Amphibia and Reptiles*. Pp. 121–122 in: Walton, D.W. (ed.) *Zoological catalogue of Australia*. Vol. 1.

Netley, South Australia: Griffin Press Ltd. vi 313 pp. [122].
Paralectotype. BMNH 1946.8.12.63, Nickol Bay, WA.

Diagnosis. As for genus.

Description of Lectotype. Adult. Moderately sized slender agamid lizard with relatively short rounded snout; head narrow and moderately elongated. Prominent canthal ridge consisting of row of enlarged heavily keeled scales. Small nasal scale and nares below ridge. Visible tympanum. A distinct neck, long limbs, long and slender tail, which is damaged and missing its end. Infralabials 11; supralabials 12. Labials elongate unkeeled. Scales on dorsal surface of head moderately heterogeneous, strongly keeled. Prominent nuchal crest of 10 enlarged scales, from ear to shoulder and extending along the back as a row of enlarge scales to base of tail. Head scales heterogeneous and strongly keeled; 4–5 enlarged white spinose scales protruding from rear of head, posterior to the jaw. Dorsal scales on body and tail mostly homogeneous and weakly to moderately keeled. Scales on thighs homogeneous and strongly keeled. Scales on the ventral surface of head strongly keeled and are weakly keeled on the body. Upper portion of head dark grey-brown and uniformly coloured. Under the head, on the chin, gular and neck dark grey pigmentation, with two pale stripes extending from back of the jaw anteriorly under chin, parallel to jaw, ending approximately half way along jaw. Broad white lip stripe, equally wide on lower and narrow upper lip, extends below ear and continues as two broad white dorsoventral stripes, extending to shoulder. Broad dorsoventral stripes intersected by three dark bands at neck, shoulders and upper back.

Variation. Adult males have dark grey to black uniform colour on top of head and below chin, onto neck and ventral surface of shoulders. However, females and juveniles often lack this uniform colour and instead have brown and black patterning on top of the head and only have flecks of grey, brown or black on their ventral surface. However, they still have two continuous dorsolateral stripes from the jaw onto the back and lack a well-defined pale stripe between the eye and the ear. Also, it is common for *Tropicagama temporalis* to have one or more broad dark lateral bands across the back at the shoulders. Commonly, the white lower lip stripe does not extend the full length of the jaw; instead, it is only present on the posterior section of the lower jaw.

Distribution and ecology. Far northern Australian coastal regions in the Northern Territory and western Cape York. Also occurs on northern offshore islands, including Indonesian islands close to Australian waters and southern Papua New Guinea. Semi-arboreal, occurring in dry tropical woodland habitats, particularly associated with coastal pandanus and paperbark watercourses. Genetic data has not yet found evidence of this species occurring on the Western Australian mainland. However, future work may find this species occurring in coastal Kimberley regions.

Remarks. *Tropicagama temporalis* is superficially similar to, and has extensive distributional overlap with, *Lophognathus gilberti* (fig. 4). *T. temporalis* is readily separated from this

species on body proportions (fig. 2) and by having two or fewer preanal pores, uniform dorsal scales with keels converging posteriorly toward midline, a prominent pale dorsolateral stripe that is broadly continuous with stripe along jaw, and lacking a well-defined pale stripe between the eye and the ear.

Identification key for *Amphibolurus*, *Chlamydosaurus* and *Lophognathus*

1. No large “frill” of skin around neck 2
 A large, loose “frill” of skin around neck
Chlamydosaurus kingii
2. Fewer than 10 femoral pores, no white spots on a black background behind the ear 3
 More than 10 femoral pores, ≥ 1 white spot on a black background behind the ear, relatively long snout and dorsoventrally compressed head, very long whip-like tail *Gowidon longirostris*
3. More than 2 preanal pores, dorsal scales heterogeneous, dorsolateral stripes discontinuous with wide pale stripe along upper or lower jaw (if present) 4
 Two or fewer preanal pores, dorsal scales uniform, with keels converging posteriorly toward midline. Prominent pale dorsolateral stripes that are broadly continuous with wide pale stripe along upper and/or lower jaw. Lacks well-defined pale stripe between eye and ear. *Tropicagama temporalis*
4. Lacks well-defined white or pale stripe extending full length between ear and eye (fig. 6), which is defined dorsally and ventrally by darker scales. Broad white stripe running extent of upper lip mostly absent 5
 Well-defined white or pale stripe extending full length between ear and eye present (fig. 6). Broad white stripe running extent of upper lip mostly present 6
5. Scales on thighs strongly heterogeneous, with scattered spinous scales and a row of small to large spinous scales running along rear of thigh 7
 Scales on thighs mostly homogeneous, lacking spinous scales on the thigh and row of enlarged spinous scales running along rear of thigh absent *Amphibolurus centralis*
6. Well-defined white spot on tympanum is present (fig. 7). It is wholly surrounded or bordered by an area of black pigmentation that runs along a raised ridge, which extends from the outer dorsoposterior edge of the tympanum towards its centre *Lophognathus horneri*
 Well-defined white spot on tympanum absent (fig. 7). If white or pale pigmentation is present on the tympanum, it is not a well-defined spot or not wholly surrounded or bordered by an area of black pigmentation that runs along a raised ridge, which extends from the outer dorsoposterior edge of the tympanum towards its centre *Lophognathus gilberti*

7. Prominent spinose nuchal and vertebral crest, and two or more additional dorsal crests. A row of large spinose scales running along rear of thigh *Amphibolurus burnsi*
Lacking multiple additional dorsal crests and row of only small spinose scales running along rear of thigh 8
8. Dark strip between nostril and eye .. *Amphibolurus norrisi*
Dark stripe between nostril and eye absent
Amphibolurus muricatus

Discussion

Molecular work, incorporating both mitochondrial and nuclear gene regions, provided compelling evidence that taxonomic revision of the genera *Amphibolurus*, *Gowidon* and *Lophognathus* was required (Melville et al., 2011). This molecular work also provided a starting point for morphological analyses, allowing us to determine diagnostic characters for each species. Until now, without the aid of molecular data, it has been difficult for taxonomists to determine which morphological characteristics were diagnostic. These past difficulties and our current study have shown that there is significant morphological homoplasy across these agamid species, with significant overlap in morphometrics, colour, patterning and scalation.

We have determined that there are four independent evolutionary lineages in the former genus *Lophognathus* (now *Gowidon*, *Lophognathus*, *Amphibolurus* and *Tropicagama*). Despite the deep divergences between the four lineages, there are extensive morphological similarities in the constituent species. In addition, the fact that we have found that the junior synonym of one *Lophognathus* species was an unrelated species, now *Amphibolurus centralis*, demonstrates the extent of homoplasy in these dragons.

It seems that most of the difficulties in determining species in these genera have occurred in northern Australia, with *Amphibolurus centralis*, *Gowidon longirostris*, *Tropicagama temporalis*, *Lophognathus gilberti* and *Lophognathus horneri* all occurring in northern and north-western Australia. This geographic concentration of taxonomic problems may result from several reasons. A lack of dedicated taxonomic research into the genera *Lophognathus* and *Amphibolurus* in northern Australia may be an important factor. There has been a paucity of taxonomic research undertaken on the Australian agamid lizards, particularly those of the Northern Territory and western Queensland. Glenn Storr from the Western Australian Museum provided much of the foundational work on the taxonomy of dragons in the arid and semi-arid regions of Australia but his taxonomic work did not include *Amphibolurus* and *Lophognathus*, except for his taxonomic review of bearded dragons and the dismemberment of the *Amphibolurus* genus (Storr, 1982). Since Storr, there has been little taxonomic work conducted on northern Australian agamids. Similar taxonomic problems have arisen in dragons occurring in the eastern states of Australia, where more research is focused. For example, Witten (1972)

described *Amphibolurus nobbi* from Queensland, New South Wales and Victoria, but more recent work has demonstrated that this species is in the genus *Diporiphora* (Edwards and Melville, 2011). Following Witten's taxonomic placement of the nobbi dragon into *Amphibolurus*, Greer (1989) noted that the colour patterns of the nobbi dragon were similar to other species of *Diporiphora*, rather than *Amphibolurus*, with a pink or rose flush to the base of the tail and yellowish sides. Thus, it appears that Witten (1972) selected characters that were not correlated with evolutionary relatedness when placing the nobbi dragon into *Amphibolurus*. Consequently, the problems with the taxonomic resolution in *Amphibolurus* and *Lophognathus* have probably resulted from a combination of little research and difficulties in morphological taxonomic research into these genera.

There is a reoccurring theme of non-diagnostic characters and morphological homoplasy in the taxonomy of Australian agamids. The use of molecular tools in the taxonomy of Amphibolurinae has greatly improved resolution and nomenclatural stability that has not been possible with morphology alone. In addition, these molecular data allow insight into evolutionary patterns in this diverse group of lizards, where there is both a high degree of morphological diversity and homoplasy across the subfamily. Our study has demonstrated the high level of morphological homoplasy across independent evolutionary lineages. Our results provide significant scope for future research into the evolutionary processes underlying the morphological convergence or parallelism in Australian agamid lizards.

Supporting information

Supplementary Appendix S1 List of museum specimens examined morphologically.

(PDF)

Acknowledgments

JM examined specimens for morphological review at the Australian Museum, Western Australian Museum, British Museum of Natural History, Museum Victoria, Museum of Comparative Zoology (Harvard University), Senckenberg Naturmuseum (Frankfurt-am-Main) and Zoological Research Museum Alexander Koenig (Bonn, Germany). JM would like to thank staff and researchers from these institutions for their help and assistance, including W. Longmore, R. O'Brien, D. Bray, P. Doughty, R. Sadlier, J. Rosado, C. McCarthy and, in particular, P. Wagner for organising type loans from other museums within Germany to be examined at the Zoological Research Museum Alexander Koenig (Bonn, Germany). We thank S. Wilson for use of images. We thank G. Shea for advice on nomenclature and discussions regarding synonymies. Research funding provided to JM by Australian Research Council and to JM, RG and JS by the Australian Biological Resources Study.

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Supplementary Appendix S1.

Voucher specimens examined

Museum abbreviations are: AM for Australian Museum Sydney, NMV for Museum Victoria Melbourne, WAM for Western Australian Museum.

Amphibolurus burnsi

NMV D52082, 8 km E of Surat, Queensland, 27° 09' S, 149° 05' E; NMV D56415, St George, Queensland, 28° 03' S, 148° 35' E; NMV D56416, St George, Queensland, 28° 03' S, 148° 35' E; NMV D74134, 10 km N of Chinchilla, Queensland, 26° 40' 23" S, 150° 35' 52" E; NMV D74135, 15 km W of Cecil Plains, Queensland, 27° 33' 29" S, 151° 03' 04" E; NMV D74137, 15 km W of Cecil Plains, Queensland, 27° 32' 44" S, 151° 04' 55" E; AM R151557, Gingham Floodplain, Te Mona, 3 km N of Allombie Bridge over Gwydir River, New South Wales, 29° 19' S, 149° 27' E; AM R151838, Kwiambal National Park, New South Wales, 29° 11' 13" S, 150° 57' 51" E; AM R155887, Brewarrina, Barwon River at West Brewarrina, New South Wales, 29° 58' S, 146° 52' E; AM R166772, Nocoleche Nature Reserve, New South Wales, 29° 51' 15" S, 144° 8' 8" E; AM R166873, AM R166874, Wanaaring township, New South Wales; AM R166910, Nocoleche Nature Reserve, New South Wales, 29° 51' 26" S, 144° 8' 9" E; AM R137612, Byerawering Property, Site 1, Banks of Culgoa River, 30 km from Goodooga Road, New South Wales, 29° 5' S, 147° 8' E; AM R148373, Macquarie Marches, Sandy Camp Property, 8 km N of Homestead on Carinda River, New South Wales, 30° 49' S, 147° 43' E; AM R153324 Yuleba State Forest (South of Condamine Hwy.), Coup 105, Queensland, 26° 54' 13" S, 149° 44' 18" E.

Amphibolurus centralis

NMV D11166, Attack Creek, Northern Territory, 18° 18' S, 134° 35' E; NMV D175, NMV D176, NMV D182, NMV D184, NMV D189, NMV D196, Alice Springs, Northern Territory, 23° 42' S, 133° 52' E; NMV D492, Illamurta, Northern Territory, 24° 18' S, 132° 41' E; NMV D72659, Buntine Highway, 20 km E of Kalkaringa, Northern Territory, 17° 24' 08" S, 130° 56' 56" E; NMV D72661, NMV D72680, Buchanan Highway, 101 km E of Top Springs, Northern Territory, 16° 45' 25" S, 132° 40' 20" E; NMV D72709, 108 km S of Cape Crawford on Tablelands Highway, Northern Territory, 17° 32' 24" S, 135° 41' 17" E; NMV D72710, 3 km S of Heartbreak Inn on Tablelands Highway, Northern Territory, 16° 42' 14" S, 135° 43' 46" E; NMV D73981, Kimberley, Duncan Road, N of Spring Creek Station, Western Australia, 16° 25' 02" S, 129° 02' 54" E; NMV D73988, Buchanan Highway S of Jasper Creek, Northern Territory, 16° 06' 55" S, 130° 53' 23" E; NMV D74005, Nutwood Road, 3 km SE, N of Daly Waters, near Scarlet Hill, Northern Territory, 16° 11' 03" S, 133° 26' 28" E; NMV D74021, Carpentaria Highway, W of Northern Territory–Queensland border, SE of Robinson River Aerodrome, Northern Territory, 16° 51' 43" S, 137° 14' 39" E; NMV D74023, Carpentaria Highway, 125 km E of Hi Way Inn, Northern Territory, 16° 28' 59" S, 134° 25' 26" E; NMV D74052, Lawn Hill Road via Gregory Downs Station, Queensland, 18° 38' 28" S, 139° 05' 55" E; NMV D74283, road to Hamilton Station Youth Camp, off Tanami Track, Northern Territory,

23° 36' 07" S, 133° 34' 36" E; NMV D74288, Red Bluff Gorge, Northern Territory, 23° 36' 07" S, 132° 30' 38" E; NMV D74673, Hodgson River Road, near Tennant Creek, 2 km E of Stuart Highway, Northern Territory, 16° 12' 18" S, 133° 25' 50" E; NMV D74695, West MacDonnell Ranges, Haast Bluff Road, Northern Territory, 23° 33' 14" S, 132° 18' 21" E.

Lophognathus gilberti

NMV D290, Arnhem Land, Oenpelli, East Alligator River, Northern Territory, 12° 19' S, 133° 03' E; NMV D34178, NMV D34179, NMV D34180, Ord River Dam area, Western Australia, 17° 24' S, 128° 52' E; NMV D5096, NMV D5123, Borrooloola, Northern Territory, 16° 04' S, 136° 18' E; NMV D5150, Arnhem Land, Upper Roper River, Northern Territory, 14° 44' S, 134° 31' E; NMV D5222, Arnhem Land, Oenpelli, Northern Territory, 12° 19' S, 133° 03' E; NMV D72579, West Arnhem Land, Yirrkakak, Northern Territory, 12° 12' 14" S, 133° 48' 04" E; NMV D72590, West Arnhem Land, Gubjekbinj, Northern Territory, 12° 15' 09" S, 133° 48' 07" E; NMV D74026, Mt Wells Road, near Grove Hill, Northern Territory, 13° 28' 47" S, 131° 32' 41" E; NMV D74027, Wells Road, near Grove Hill Station, Northern Territory, 13° 28' 42" S, 131° 32' 13" E; NMV D74258, 20 km N of Katherine, Stuart Highway, Northern Territory, 14° 18' 57" S, 132° 06' 18" E; NMV D74260, Mount Wells, Northern Territory, 13° 40' 25" S, 132° 48' 26" E; NMV D74263, road to Umbarrumba Gorge, S of Pine Creek, Northern Territory, 13° 51' 19" S, 131° 49' 14" E; NMV D74280, Mount Wells Road, Northern Territory, 13° 29' 31" S, 131° 34' 25" E; NMV D74281, NMV D74282, Mount Wells Road, Northern Territory, 13° 29' 33" S, 131° 36' 44" E; NMV D74286, off Stuart Highway, 42 km N of Katherine, Northern Territory, 14° 11' 12" S, 132° 01' 52" E; NMV D74289, NMV D74293, Umbrawarra Gorge, Northern Territory, 13° 57' 14" S, 131° 41' 39" E; NMV D74298, Marrakai Road, about 8 km SW of Arnhem Highway, Northern Territory, 12° 47' 59" S, 131° 26' 38" E. WAM R126027, WAM R126029, WAM R126031, 4 km SW of Point Spring Yard, Western Australia, 15° 25' 35" S, 128° 51' 09" E; WAM R163559, Anjo Peninsula, Western Australia, 14° 04' 19" S, 126° 24' 27" E.

Gowidon longirostris

NMV D222, NMV D224, NMV D231, NMV D235, Central Australia, Dalhousie (original label in Spencer's writing "Dalhousie"), Northern Territory, 26° 30' S, 135° 28' E; NMV D2336, NMV D3481, Finke River, Northern Territory, 25° 02' S, 134° 24' E; NMV D239, Derwent Creek, Northern Territory, 17° 34' S, 145° 13' E; NMV D4945, NMV D4946, Central Australia, Barrow Creek, Northern Territory, 21° 32' S, 133° 53' E; NMV D50509, NMV D50510, NMV D50511, Todd River, Alice Springs, Northern Territory, 23° 48' S, 134° 25' E; NMV D50537, Emily Gap, MacDonnell Ranges, Northern Territory, 23° 45' S, 133° 57' E; NMV D509, NMV D510, NMV D511, Charlotte Waters, Northern Territory, 25° 56' S, 134° 53' E; NMV D5383, NMV D5384, no data; NMV D56308, Alice Springs, Northern Territory, 23° 42' S, 133° 52' E; NMV D67487, Finke River, Northern Territory, 25° 02' S, 134° 24' E; NMV D67644, Simpsons Gap, Northern Territory, 23° 42' 07" S, 133° 43' 05" E; NMV D67663, NMV D67665, NMV D67668, Ellery Creek, Northern Territory, 23° 47' 10" S, 133° 04' 07" E; NMV D67669, NMV D67670, NMV D67671, NMV D67672, NMV D67703,

Serpentine Gorge, Northern Territory, 23° 45' 25" S, 132° 58' 24" E; NMV D67713, NMV D67714, Ormiston Pound, near creek, Northern Territory, 23° 37' S, 132° 48' E; NMV D67758, Finke River, Palm Valley, old rangers' station, Northern Territory, 24° 03' 21" S, 132° 45' 22" E; NMV D67764, NMV D67765, NMV D67766, Palm Valley, Finke River, Northern Territory, 24° 02' 33" S, 132° 42' 22" E; NMV D67777, NMV D67778, Finke River, Palm Valley, Red Gum site near old rangers' station, Northern Territory, 24° 03' 06" S, 132° 45' 18" E; NMV D67786, Central Australia, waterhole, 3.4 km from Boggy Hole, Northern Territory, 24° 08' 07" S, 132° 50' 07" E; NMV D69, NMV D70, Tennant Creek, Northern Territory, 19° 39' S, 134° 11' E; NMV D72733, Todd River, East MacDonnell Ranges, Northern Territory, 23° 47' 45" S, 134° 18' 42" E; NMV D74269, Ormiston Gorge, Northern Territory, 23° 37' 56" S, 132° 43' 39" E; NMV D74317, Great Northern Highway, 1 km E of Roebuck Roadhouse at entrance to Kilito Station, Western Australia, 17° 48' 57" S, 122° 40' 44" E; NMV D74368, NMV D74370, NMV D74371, Great Northern Highway, N of Sandfire Roadhouse, Stanley picnic stop, Western Australia, 19° 02' 35" S, 121° 39' 57" E; NMV D74391, Pilbara, Ingee Station, off Great Northern Highway, Western Australia, 20° 46' 42" S, 118° 31' 33" E; NMV D74407, Great Northern Highway, South Gascoyne River, 64 km S of Kumarina Roadhouse, Western Australia, 25° 12' 09" S, 119° 20' 05" E; NMV D74408, Great Northern Highway, South Gascoyne River, 64 km S of Kumarina Roadhouse, Western Australia, 25° 12' 09" S, 119° 20' 05" E; NMV D74426, Tjukayiria Roadhouse, about 3 km W, Warburton Hwy, Western Australia, 27° 09' 57" S, 124° 32' 54" E; NMV D95, NMV D96, NMV D97, Oodnadatta, South Australia, 27° 33' S, 135° 27' E.

***Lophognathus horneri* sp. nov.**

NMV D10440, NMV D10441, NMV D10442, NMV D10443, NMV D10444, NMV D10838, NMV D10887, Timber Creek, Northern Territory, 15° 39' S, 130° 29' E; NMV D2360, NMV D2365, Port George IV, Western Australia, 15° 22' S, 124° 39' E; NMV D2934, NMV D5630, Tennant Creek, Northern Territory, 19° 39' S, 134° 11' E; NMV D72638, NMV D72652, Montejinni Creek, Buntine Highway, Northern Territory, 16° 38' 06" S, 131° 45' 20" E; NMV D72643, Willaroo Station, Top Springs, track off Victoria Highway, Northern Territory, 15° 18' 55" S, 131° 34' 10" E; NMV D72658, Kelly Creek, Wave Hill Homestead, Northern Territory, 17° 23' 08" S, 131° 06' 44" E; NMV D73807, NMV D73809, NMV D73810, NMV D73811, Kimberley, Gibb River Road crossing of the Durack River, Western Australia, 15° 58' 26" S, 127° 09' 13" E; NMV D73818, Kimberley, Gibb River Road, 10 km W of Ellenbrae Station, Western Australia, 15° 59' 27" S, 126° 57' 10" E; NMV D73820, Kimberley, Gibb River Road, 8 km W of Ellenbrae Station, Western Australia, 15° 59' 24" S, 127° 00' 16" E; NMV D73845, NMV D73846, Kimberley, Mitchell Plateau, King Edward River Camp, Western Australia, 14° 52' 57" S, 126° 12' 10" E; NMV D73851, Kimberley, Gibb River Road, 1 km W of the Kalumburu turn-off, Western Australia, 16° 09' 19" S, 126° 30' 10" E; NMV D73863, Kimberley, Mt Elizabeth, Western Australia, 16° 13' 59" S, 125° 59' 21" E; NMV D73867, Kimberley, Gibb River Road, W of Snake Creek, Western Australia, 16° 32' 15" S, 126° 15' 29" E; NMV D73886, Kimberley, Derby Caravan Park, Western Australia, 17° 18' 30" S, 123° 37' 44" E; NMV D73967,

Kimberley, Duncan Road, N of Spring Creek Station, Western Australia, 16° 19' 43" S, 129° 03' 33" E; NMV D73984, Buchanan Highway S of Jasper Creek, Northern Territory, 16° 02' 45" S, 130° 51' 59" E; NMV D74259, Stuart Memorial, Stuart Highway, Northern Territory, 19° 01' 24" S, 132° 08' 30" E; NMV D74271, Stuart Memorial, 48 km N of Three Ways, Stuart Highway, Northern Territory, 19° 01' 24" S, 134° 08' 30" E; NMV D74309, NMV D74312, Wolfe Creek, Tanami Road, Western Australia, 18° 59' 44" S, 127° 41' 52" E; NMV D74334, Derby, road to Prison Boab Tree, Western Australia, 17° 21' 04" S, 123° 40' 09" E; NMV D74362, NMV D74363, NMV D74364, 80 Mile Beach Caravan Park, 50 km S of Sandfire, Western Australia, 19° 45' 16" S, 120° 40' 20" E; NMV D74683, road to Karundi, 35 km E of Stuart Highway, Northern Territory, 20° 28' 22" S, 134° 28' 51" E; NMV D74687, road to Davenport Ranges National Park, near Tennant Creek, Northern Territory, 20° 37' 34" S, 134° 47' 14" E; NMV D74690, road to Davenport Ranges National Park, near Tennant Creek, Northern Territory, 20° 38' 28" S, 134° 46' 42" E; WAM R102296, WAM R102307, Hermite Island (South), Montebello Islands, Western Australia, 20° 28' 00" S, 115° 31' 00" E; WAM R102321, Ah Chong Island, Montebello Islands, Western Australia, 20° 31' 00" S, 115° 33' 00" E; WAM R108806, Calico Springs, Western Australia, 17° 17' 00" S, 128° 11' 00" E; WAM R113222, South Muiron Island, Western Australia, 21° 42' 00" S, 114° 48' 00" E; WAM R113987, King Edward River, Western Australia, 14° 55' 00" S, 126° 12' 00" E; WAM R114385, Coulomb Point Nature Reserve, Western Australia, 17° 22' 00" S, 122° 09' 00" E; WAM R131275, Fitzroy Crossing, Western Australia, 18° 10' 58" S, 125° 36' 00" E; WAM R131990, Kununurra, Western Australia, 15° 48' 00" S, 128° 43' 00" E; WAM R132850, Kununurra, Western Australia, 15° 47' 38" S, 128° 43' 11" E; WAM R132851, Kununurra, Western Australia, 15° 47' 38" S, 128° 43' 11" E; WAM R139477, WAM R139481, Potter Island, Western Australia, 20° 56' 15" S, 116° 09' 10" E; WAM R141302, Cape Preston Area, Western Australia, 20° 52' 59" S, 116° 11' 41" E.

Tropicagama temporalis

NMV D14455, NMV D14456, NMV D14457, NMV D14458, NMV D14459, NMV D14460, NMV D14461, Gulf Province, Balimo, Papua New Guinea, 08° 00' S, 142° 55' E; NMV D2289, NMV D2293, NMV D3732, NMV D3733, NMV D5924, NMV D5925, Borebada (as "Bora Bada, New Guinea"), 09° 28' S, 147° 12' E; NMV D4551, Northern Territory; NMV D49838, NMV D49839, NMV D49840, NMV D49841, NMV D49842, NMV D49889, NMV D50083, NMV D50084, NMV D50085, NMV D50086, NMV D50087, NMV D50088, NMV D50089, Gulf Province, Aramia River, Awaba, Papua New Guinea, 08° 01' S, 142° 45' E; NMV D5234, Melville Island, Northern Territory, 11° 27' S, 130° 47' E; NMV D5517, Darwin, Northern Territory, 12° 27' S, 130° 50' E; NMV D6655; NMV D74299, Marrakai Road near Heather Lagoon, Northern Territory, 12° 54' 40" S, 131° 12' 24" E; NMV D74306, NMV D74307, Darwin, Malack, Wescombe Court, Northern Territory, 12° 23' 26" S, 130° 54' 24" E; NMV D74311, NMV D74313, NMV D74314, NMV D74318, NMV D74319, Darwin, gardens at Museum and Art Gallery of the Northern Territory, Northern Territory, 12° 26' 16" S, 130° 50' 03" E.

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Recognising variability in the shells of argonauts (Cephalopoda: Argonautidae): the key to resolving the taxonomy of the family

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Abstract

Finn, J.K. 2018. Recognising variability in the shells of argonauts (Cephalopoda: Argonautidae): the key to resolving the taxonomy of the family. *Memoirs of Museum Victoria* 77: 63–104.

Argonauts (Cephalopoda: Argonautidae) are a family of pelagic octopuses that are most commonly recognised by the beautiful white shells of females (known as paper nautilus), prized by beachcombers the world over. Taxonomic delineation of the group has historically relied exclusively on features of the shells of females and has resulted in more than 50 species names being coined worldwide. This approach has created considerable confusion in the taxonomy of the family because argonaut shells are not true molluscan shells and display considerable variation in form. This study closely examined a large number of argonaut shells from museum collections throughout the world. Two types of shell formation that had been previously attributed to separate argonaut species were recognised within individual shells. It is proposed here that the different shell forms reflect the effects of ecological or biological factors or events, often manifesting as dramatic changes in shell growth and shape within the development of an individual shell. The resulting combinations of shell formation types clearly explain both the extreme variation observed across large numbers of argonaut shells and the high number of nominal species names coined in the past. Researchers coining new fossil argonaut species based solely on shell characters are advised to proceed with caution. This study supports parallel morphological and molecular research recognising the existence of only four extant argonaut species worldwide: *Argonauta argo*, *A. hians*, *A. nodosus* and *A. nouryi*.

Keywords

paper nautilus, *Argonauta argo*, *Argonauta hians*, *Argonauta nodosus*, *Argonauta nouryi*, Coleoidea, Octopoda, shell morphometrics

Introduction

Argonauts (Cephalopoda: Argonautidae) are a family of pelagic octopuses that inhabit tropical and temperate oceans of the world (fig. 1). Derived from benthic octopus ancestors, argonauts have departed the sea floor to carry out their entire life cycle in the open ocean (Young et al., 1998). Argonauts are most widely recognised by the beautiful white shells of females that are commonly known as paper nautilus and are prized by beachcombers the world over. These shells function as both brood chambers for the females' eggs (Naef, 1923) and hydrostatic structures by which female argonauts are able to attain neutral buoyancy (Finn and Norman, 2010).

Images of argonaut shells have a long history, adorning artefacts dating back to Minoan civilisations (3000–1050 BC; Walters, 1897; Mackeprang, 1938; Hughes-Brock, 1999) and featuring in the earliest conchological works (e.g. Rumphius, 1705; Argenville, 1742; Gualtieri, 1742; Seba, 1758; Martini, 1769). By contrast, the identity of the occupant of the shell (i.e. the argonaut) has remained largely unknown or misinterpreted. For example, in the early 1800s it was widely believed that the octopus commonly found in the argonaut shell was not the rightful owner, but was a parasite having

devoured the original occupant (Sowerby and Sowerby, 1820–1825; Broderip, 1828).

In the absence of knowledge about the animals that created the shells, a taxonomic system that relied completely on shell features arose for the family. Variations in shell shape and appearance formed the basis of new species descriptions, giving rise to 53 species names and 11 subspecies names worldwide (Sweeney and Young, 2004).

At the core of this taxonomic system is the issue that argonaut shells display a considerable degree of variability. This variability has been observed across shells produced by individuals of the same species (Voss and Williamson, 1971) and even between opposing faces of the same shell (Cotton and Godfrey, 1940; Trego, 1992). This variability is likely to be exacerbated by the female argonaut's ability to repair (Power, 1856; Hoyle, 1886; Boletzky, 1983; Trego, 1993) and completely rebuild the shell (Holder, 1909a, 1909b; Alliston, 1983).

Argonaut shells are not true molluscan shells. Unlike the shells of other molluscs (e.g. gastropods), argonaut shells are not produced by the derivatives of the shell field (the mantle epithelium responsible for shell secretion in other molluscs; see Kniprath, 1981). In argonauts, the shell field disappears during embryonic development (Kniprath, 1981). The argonaut



Figure 1. Live female argonaut (*Argonauta argo*) observed swimming close to the ocean surface and holding her white paper nautilus shell that functions as a brood chamber for the female's eggs and as a hydrostatic structure for maintaining neutral buoyancy.

shell is a secondary calcium carbonate structure secreted from webs on the distal ends of the female argonaut's first (dorsal) arm pair.

Female argonauts commence forming shells approximately 12 days after hatching (*A. argo*: Power in Roberts, 1851; Power in Catlow, 1854) at a size of approximately 5–7 mm mantle length (*A. argo*: Jatta, 1896; Naef, 1923; *A. hians*: Nesis, 1977; *A. nouryi*: Finn, 2009). The initial shell is formed without sculpturing (Jatta, 1896). By the time the female argonaut reaches 10 mm mantle length, the shell (which is now 14 mm in length) is fully formed (*A. hians*: Nesis, 1977). The webs on the female's dorsal arms overlap the edge of the shell and add to it as the female grows. Irregularities in the lay of the web along the shell edge is presumed to cause the undulations in the surface of the shell, visible as radiating ridges (or ribs) in fully formed shells (Mitchell et al., 1994).

Once the female argonaut reaches maturity, she lays long strands of eggs that are attached to the internal central axis of the shell. Female argonauts are continuous spawners (Boletzky, 1998; Rocha et al., 2001; Laptikhovsky and Salman, 2003) with asynchronous ovulation and monocyclic spawning (i.e. egg-laying occurring over an extended and continuous spawning period in relation to the animal's life; Rocha et al., 2001). Spawning is thought to extend over several months (Boletzky,

1998) and based on published counts, proposed spawning frequencies and proposed spawning durations, it has been surmised that the potential fecundity of a female *A. argo* could exceed one million eggs (Laptikhovsky and Salman, 2003).

To stabilise argonaut taxonomy, the aim of this study was to examine the inter- and intra-specific variation in argonaut shell shape. Four key species (identified from morphological studies; see Finn, 2013, 2016) and shells at the centre of taxonomic confusion for these species were targeted. These target groups were the *Argonauta nouryi/cornutus* complex, the *A. hians/boettgeri* complex, the *A. nodosus/tuberculatus* complex and *A. argo*. This study supports parallel morphological and molecular research recognising the existence of only four argonaut species worldwide: *A. argo* Linnaeus, 1758; *A. hians* [Lightfoot], 1786; *A. nodosus* [Lightfoot], 1786; and *A. nouryi* Lorois, 1852.

Materials and methods

More than 1500 argonaut shells were examined over the course of this project. Most of the shells examined reside in museum collections within Australia, South Africa, Europe and the United States. Institutions visited include: Australian Museum, Sydney, Australia (AMS); Academy of Natural

Sciences, Philadelphia, USA (ANSP); The Natural History Museum, London, UK (BMNH); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museums Victoria, Melbourne, Australia (NMV); Queensland Museum, Brisbane, Australia (QMB); South African Museum, Cape Town, South Africa (SAM); South Australian Museum, Adelaide, Australia (SAMA); Santa Barbara Museum of Natural History, Santa Barbara, USA (SBMNH); Tasmanian Museum and Art Gallery, Hobart, Australia (TMAG); National Museum of Natural History, Smithsonian Institution, Washington, USA (USNM); Western Australian Museum, Perth, Australia (WAM). Material loaned from the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM) was examined at NMV.

While all shells examined ultimately helped in the formation of ideas and an understanding of shell shape variation, two large collections were pivotal in enabling argonaut shell variability to be interpreted.

The first lot, is a large collection of beach-cast argonaut shells collected by Andrés Gonzalez-Peralta (*Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, MEXICO*) on the beach at El Mogote, La Paz, Baja California Sur, Mexico, North America, 24° 10' 00" N, 110° 24' 00" W, during the winters of 2000 and 2005. These shells are lodged in the collection of SBMNH with the following registration numbers: 172 *Argonauta* shells collected on 15 January 2000 – SBMNH 345766 (93 shells), SBMNH 345767 (15 shells) and SBMNH 345768 (64 shells); 92 *Argonauta* shells collected on 31 January 2005 – SBMNH 357476 (77 shells) and SBMNH 357475 (15 shells).

The second lot was obtained by chance when researchers on a research expedition off Rowley Shoals, Western Australia left a pelagic trawl net in the water while steaming between two stations: north-east of Mermaid Reef (Stn. 10, 17° 23' S, 118° 52' E) and south-west of Imperieuse Reef (Stn. 11, 16° 53' S, 119° 53' E). This occurred on board the FV *Courageous* on 18–19 August 1983. On recovering the net, researchers P. Berry and N. Sinclair were surprised to find 73 female argonauts with intact shells. Two specimens were lodged in NMV while the remainder were retained by WAM. The collection records of these lots are as follows: 71 female argonauts – WAM S31520; 2 female argonauts – NMV F87104.

Shell terminology and measurements follow Finn (2013). The opening of the shell is termed the *aperture* while the left and right sides of the shell are termed *lateral faces*. An extension of the axial thickening beyond the surface of the lateral face of the shell is termed an *ear*. The lateral faces are adorned with *ribs* radiating from the central axis of the shell towards the *keel*. Ribs may be *smooth* (i.e. continuous) or *tuberculated* (i.e. consisting of raised separate tubercles). The keel is bordered by two opposing rows of *keel tubercles*. The keel surface may be *concave*, *straight* or *convex*. The presence of tubercles on the keel surface is known as *inter-keel tuberculation*. To allow quantitative comparison of a large number of shells, a set of standard measurements was taken. These measurements included: shell length (ShL), maximum length of shell (note that P indicates that the ShL measurement was taken from a scaled digital photograph of the shell, not

directly from the shell); shell weight (ShW), weight (grams) of dry shell; shell breadth (ShB), maximum breadth of the shell; rib count (RC), number of ribs adorning a single lateral face, counted around the keel and aperture edge; ear width (EW), external measurement between lateral tips of opposing ears; aperture length (ApL), internal distance from the axial thickening to the ventral keel surface; aperture width (ApW), internal measurement between two opposing lateral walls at widest point; keel width (KW), external measurement of keel at ventral most position; keel tubercle count (KTC), number of keel tubercles counted around a single face (see fig. 2).

Scatter plots of measurements against ShL were used to assess differences across large numbers of shells. Regression lines were plotted using Microsoft Excel for Mac 2011. Analysis of covariance (ANCOVA) was performed using Systat 13.2 to assess the significance of the difference between the slopes of the regression lines.

Scanning electron microscopy was used to examine shell microstructure and allow accurate measurement of shell thickness. Shell sections were placed in a sonicator bath for short periods (5–10 seconds) to dislodge any debris, allowed to air-dry, then placed onto double-sided carbon tabs (Ted Pella, Redding) and sputter coated with gold. Scanning electron micrographs were taken using a Zeiss EVO 40 XVP (Zeiss, Cambridge) housed at SBMNH.

Where female argonauts could be definitively linked with shells, a set of soft body measurements was taken following Finn (2013). These measurements included: dorsal mantle length (DML), length from posterior tip of mantle to furrow between mantle edge and base of first arms; mantle width (MW), lateral width of mantle at widest point; head width (HW), lateral width of head measured between the opposing eye surfaces; arm length (AL), length of arm from the edge of the mouth to arm tip, measured along the face of the arm using a piece of string (for arms 2–4); funnel length (FL), distance from the anterior tip of the funnel to the posterior medial margin. The relationship between features of female argonauts and their shells were examined using scatter plots and linear regression.

Results

Argonauta nouryi Lorois, 1852; the *A. nouryi/cornutus* complex

In spring each year, small argonauts wash up in large numbers on beaches in the southern Gulf of California (Gonzales-Peralta in Saul and Stadum 2005). These small argonauts are regularly attributed to two species: *A. nouryi* Lorois, 1852 and *A. cornutus* Conrad, 1854¹ (Garcia-Dominguez and Castro-Aguirre 1991; Gonzales-Peralta 2006).

A. nouryi was described by Lorois in 1852. The identification of this species resides solely in features of the shell, which is described as elliptical with numerous fine lateral ribs and weak keel tubercles. Fig. 3 incorporates a

1 A third large form also washes up on southern Gulf of California beaches in spring and is regularly attributed to the species *A. pacificus*, a synonym of *A. argo*; see Finn (2013) for details.

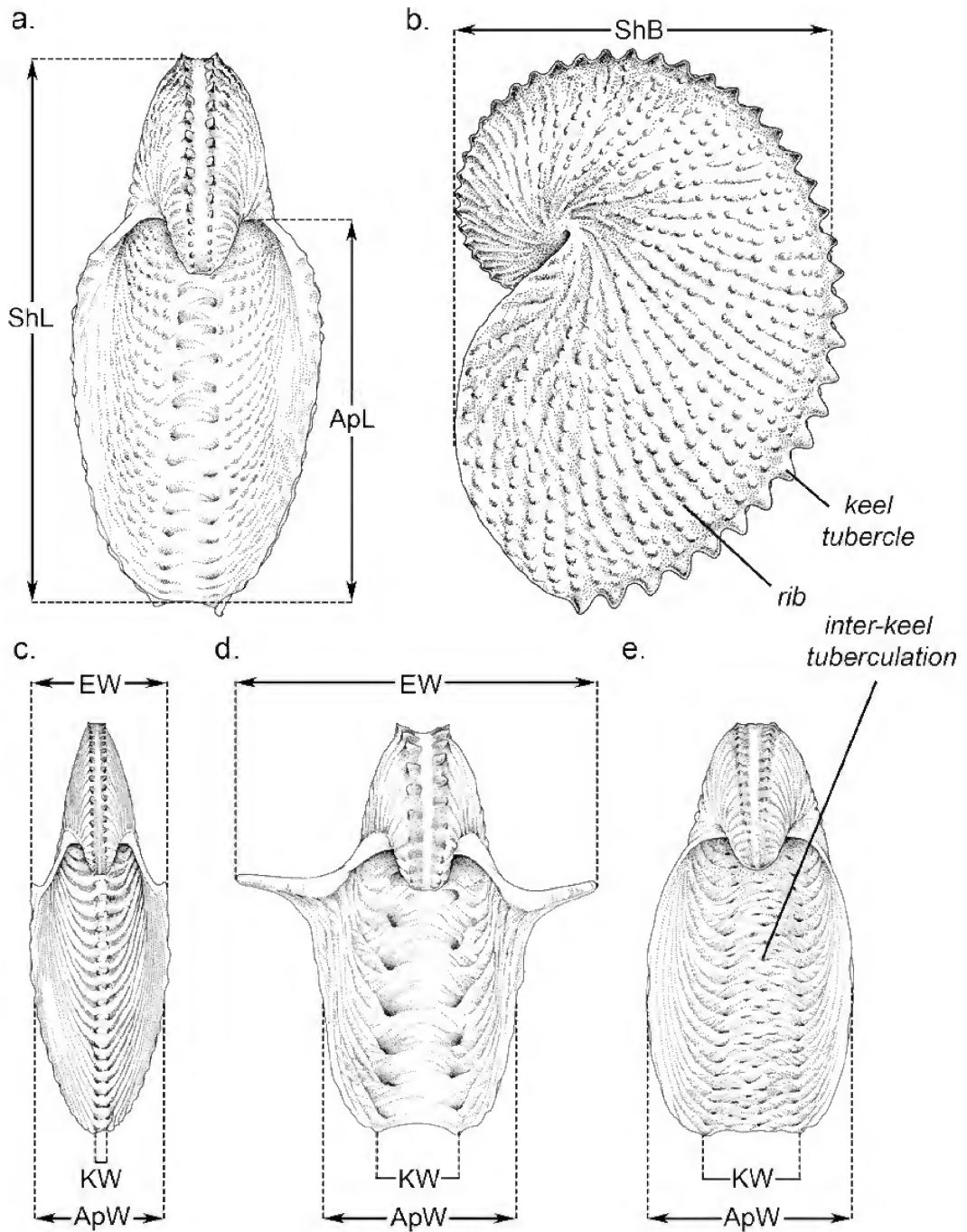


Figure 2. Argonaut shell measurements and terminology, following Finn (2013): a, *Argonauta nodosus* aperture view (NMV F164695); b, *A. nodosus* lateral view (NMV F164695); c, *A. argo* aperture view (WAM S31503); d, *A. nouryi* aperture view (SBMNH 345766, specimen #074); e, *A. nouryi* aperture view (SBMNH 345768, specimen #109). Abbreviations: ApL = aperture length; ApW = aperture width; EW = ear width; KW = keel width; ShB = shell breadth; ShL = shell length. Illustrations: R. Plant.

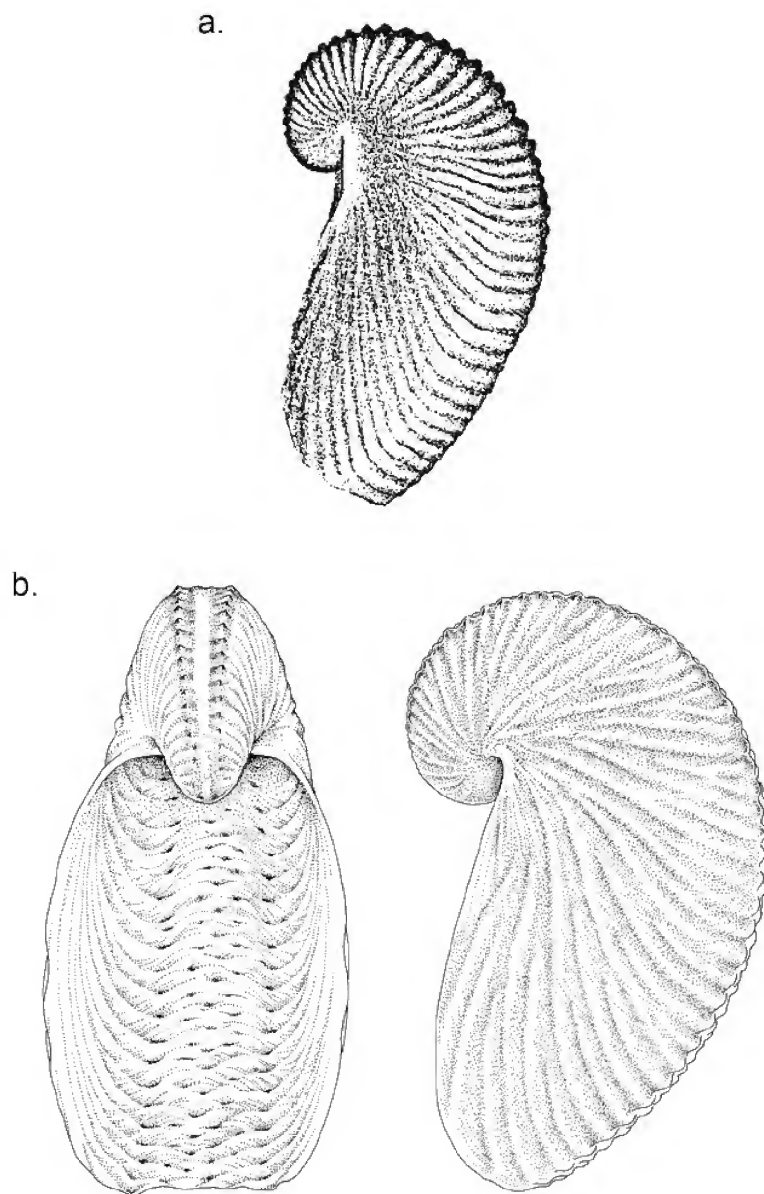


Figure 3. Comparison of a shell from the examined SBMNH lot with an illustration taken from the original description of *Argonauta nouryi* Lorois, 1852: a, reproduction of the illustration from the original description of *A. nouryi* Lorois, 1852, plate 1, fig. 5; b, illustrations of a shell matching the description of *A. nouryi* taken from the examined lot (shell #109, 66.5 mm shell length, SBMNH 345768). Illustration: R. Plant. Scale bar = 1 cm.

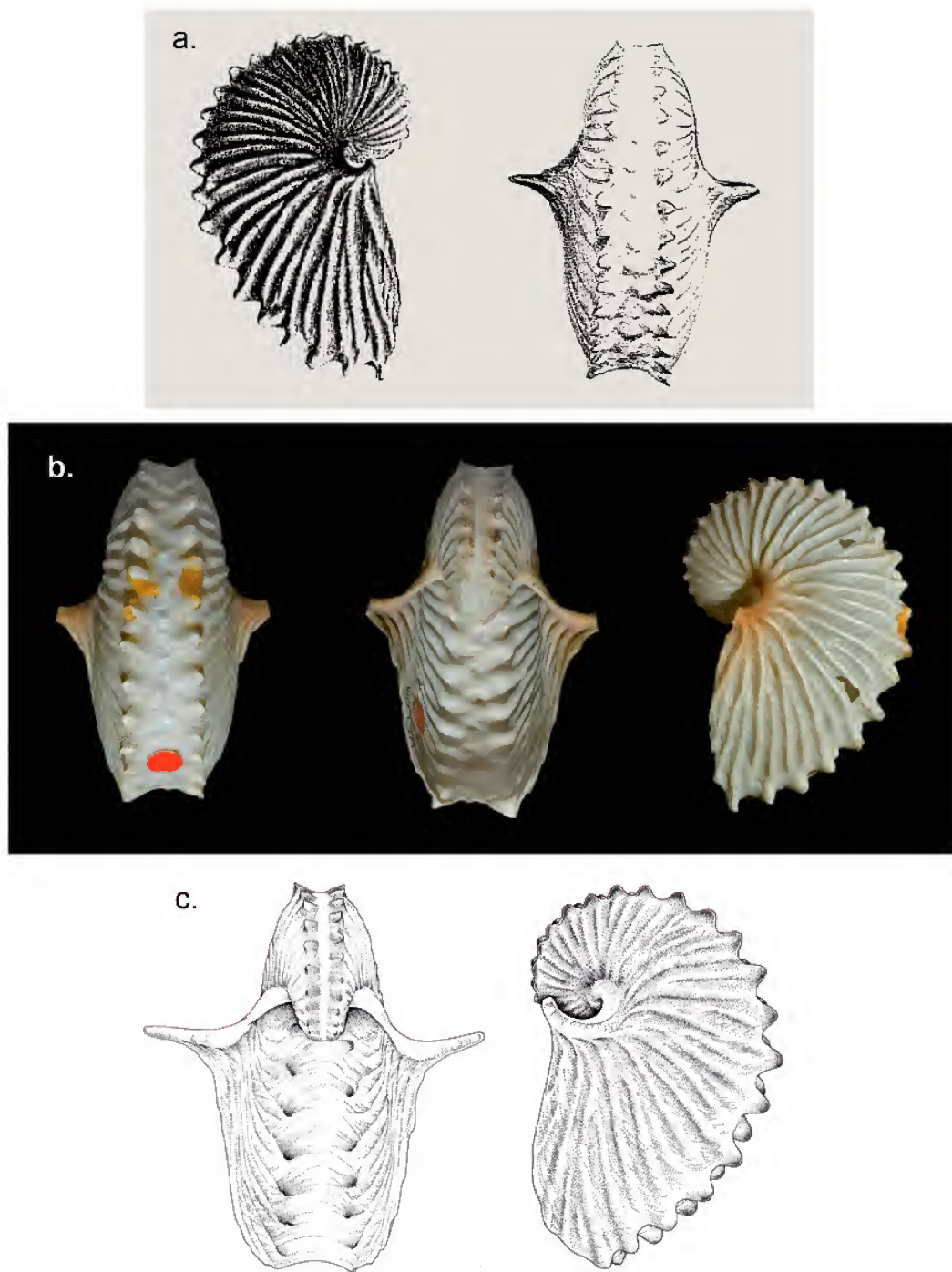


Figure 4. Comparison of a shell from the examined SBMNH lot with the type specimen and illustrations taken from the original description of *Argonauta cornutus* Conrad, 1854: a, reproduced illustration taken from the original description of *A. cornutus* Conrad, 1854, plate 34, fig. 2; b, photographs of the type specimen illustrated in the original description (58.6 mm shell length, ANSP 63496; please note, the original description illustrations mirror the characters of the shell, most likely due to the engraving and printing process of the era); c, illustrations of a shell matching the description of *A. cornutus* taken from the examined lot (shell #74, 65.0 mm shell length, SBMNH 345766). Illustration: R. Plant. Scale bar = 1 cm.

reproduction of the illustration presented by Lorois, 1852 (plate 1, figure 5), and illustrations of a shell from the Gulf of California that is consistent with the original description (shell #109, SBMNH 345768). According to Keen (1971) “the ‘shell’ is more elliptical than that of *A. cornutus*, with only the early part of the coil moderately well tinged with brown along the wide and weak tuberculate keel. The surface is delicately ribbed and has a finely granular texture” (p. 895). Voss (1971) believed that “*Argonauta nouri* is a distinctive species [...]”. The shells are longer than in any other species of *Argonauta*, the ribs are more numerous, there are no distinct tubercles marking the edges of the carinal area; the carina is wide, very convex, and covered by numerous, small, blunt tubercles formed by the crisscrossing of the ribs” (p. 32).

Argonauta cornutus was described by Conrad in 1854. The identification of this species also resides solely in features of the shell, which is described as having a broad keel, large keel tubercles and large ears. Fig. 4 incorporates a reproduction of the illustration presented by Conrad, 1854 (plate 34, figure 2), photographs of the type specimen (ANSP 63496) and illustrations of a shell from the Gulf of California that is consistent with the original description (shell #74, SBMNH 345766). According to Keen (1971), “the surface of the yellowish-white ‘shell’ is finely granular, the spines and part of the spire dark brown, the keel relatively broad, and the two long axial expansions suffused with purplish brown” (p. 894). Voss (1971) summarised that “*Argonauta cornutus* seems best characterised by the few radial ribs, the presence of fine sharp tubercles or papillae over the sides of the shell, the few rather sharp, large carinal tubercles on each side, the convex carinal surface, and the few, large, blunt tubercles on the carinal surface between the two rows of carinal boundary tubercles” (p. 32).

The distributions of these two species are reported to overlap, with *A. cornutus* known from the Gulf of California to Panama and *A. nouri* being widespread in the equatorial Pacific, ranging from the west coast of Southern California to Peru (Keen 1971).

A mixed lot

As described in the Materials and Methods section above, the 157 shells in the collection at SBMNH were collected on the same beach in Baja California on the same day. These shells had previously been identified as representing both *A. cornutus* and *A. nouri* and were registered accordingly: SBMNH 345766, *Argonauta cornutus* 93 shells; SBMNH 345768, *Argonauta nouri*, 64 shells.

Initial examination of the lots indicated that the shells had been attributed to either *A. cornutus* or *A. nouri* based on the presence or absence of ears – a character historically attributed to only *A. cornutus*. Further examination of the lot revealed that separation of the shells into two distinct groups (i.e. either *A. cornutus* or *A. nouri*) was not as straightforward as first thought. While some shells within the lot displayed all the characters associated with either *A. cornutus* or *A. nouri*, the lot also appeared to contain shells with combinations of the attributes of the two shell types. To illustrate this variation, three shells of similar size but varied appearance were selected. Fig. 5 presents photographs of these three shells from multiple perspectives:

- Shell #74 (SBMNH 345766), *cornutus*-type voucher (fig. 5a, i–iv and fig. 4c). Shell morphometrics: ShL 65.0; ShW 4.0; ShB 40.7; RC 45; EW 58.1; ApL 45.9; ApW 28.4; KW 15.6; KTC 27.
- Shell #42 (SBMNH 345766), *intermediate* voucher (fig. 5b, i–iv). Shell morphometrics: ShL 61.2; ShW 3.1; ShB 36.4; RC 47; EW 36.1; ApL 43.1; ApW 30.9; KW 14.0; KTC 32.
- Shell #109 (SBMNH 345768), *nouri*-type voucher (fig. 5c, i–iv and fig. 3b). Shell morphometrics: ShL 66.5; ShW 2.4; ShB 39.9; RC 54; EW (28.3); ApL 48.8; ApW 32.5; KW 15.8; KTC 54.

While it would be straightforward to attribute shell #74 (fig. 5a) to *A. cornutus* Conrad, 1854, and shell #109 (fig. 5c) to *A. nouri* Lorois, 1852, placement of shell #42 (fig. 5b) presents problems. While shell #42 possesses the aperture shape of *A. cornutus*, it lacks its protruding ears. While shell #42 possesses the keel tuberculation and reduced ventral keel tubercles of *A. nouri*, its dorsal keel tubercles are large and pronounced.

To determine whether there was a significant difference between eared and earless shells within the lot, a quantitative approach was undertaken. All intact shells within the lot were individually measured and weighed. All shells were designated as being either eared or earless based on the relative EW and ApW measurements. Because EW is an external measurement (i.e. measured across the extremities of the opposing ears) and ApW is an internal measurement (i.e. measured between the lateral walls of the shell), 1.0 mm was added to the ApW to accommodate for the thickness of the lateral walls of the shell. Shells were classified as follows:

- eared = $EW > ApW + 1.0 \text{ mm}$ (103 shells)
- earless = $EW \leq Apw + 1.0 \text{ mm}$ (35 shells).

Scatter plots were generated to compare eared and earless shells for all measured characters. Characters of primary interest were those previously reported to distinguish *A. cornutus* and *A. nouri*.

Shell shape. The most universally recognised character of *A. nouri* is reportedly the elliptical shape of the shell: “The whorls increase in size very rapidly and the last is very elongate. Viewed laterally it is much shallower than is usual in the genus” (Robson, 1932, p. 198). The shells are said to be “more elliptical than that of *A. cornutus*” (Keen, 1971, p. 895) and “longer than in any other species of *Argonauta*” (Voss, 1971a, p. 33).

To investigate variation in shell shape across the lot, ShB was plotted against ShL (fig. 6). Probability plots indicate that both ShB and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ShB the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in shell shape exists between eared and earless shells ($F_{(1,136)} = 5.58, p = 0.02$).

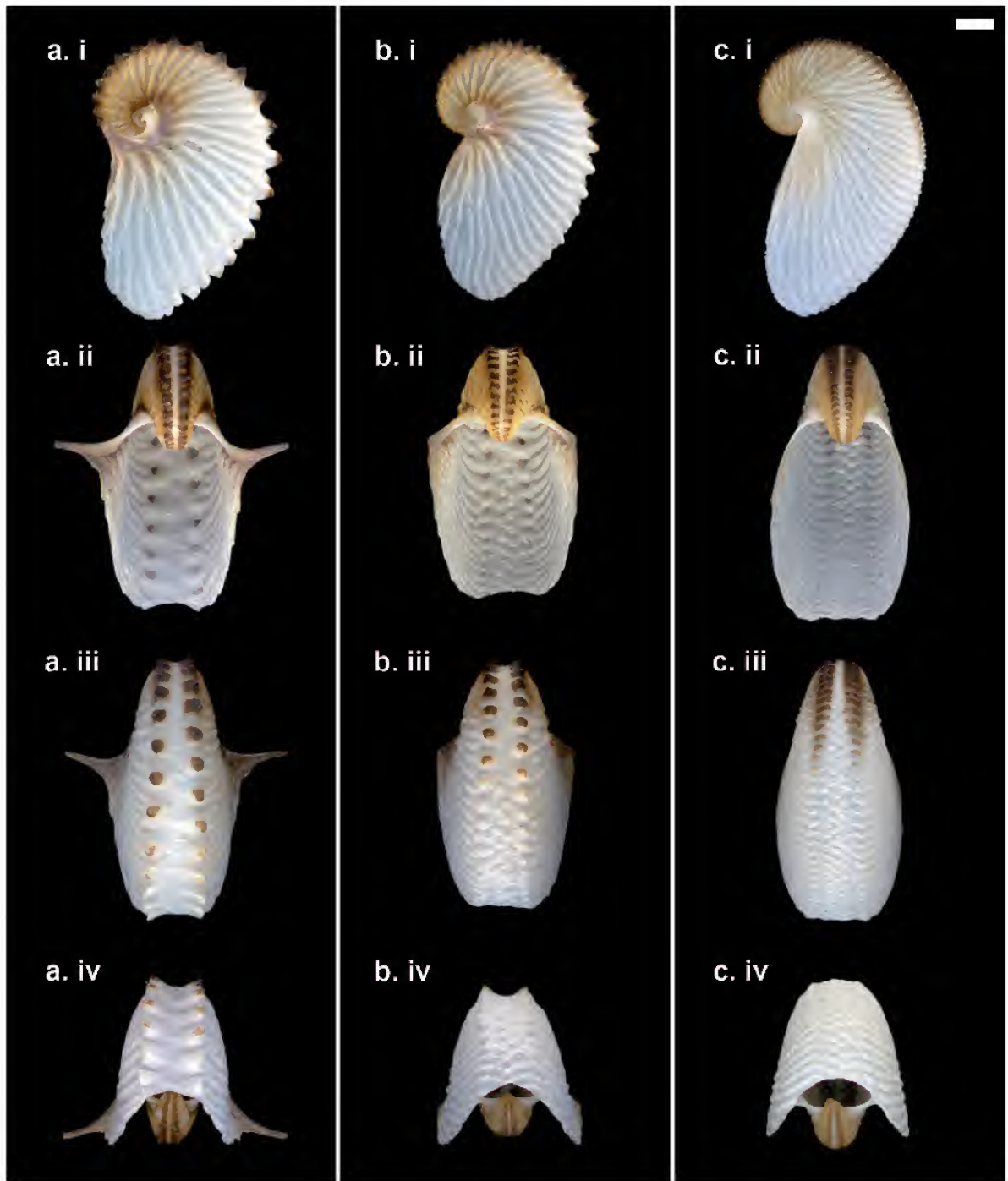


Figure 5. Three similarly sized shells of varied appearance selected from the examined SBMNH lot: a–c, three similarly sized shells of varied appearance selected from the single lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000; a, shell #74 (65.0 mm shell length, SBMNH 345766) assigned the name *cornutus-type voucher*; b, shell #42 (61.2 mm shell length, SBMNH 345766) assigned the name *intermediate voucher*; c, shell #109 (66.5 mm shell length, SBMNH 345768) assigned the name *nouryi-type voucher*; i–iv, multiple perspectives of each shell; i, left lateral view; ii, anterior aperture view; iii, posterior keel view; iv, ventral view. Scale bar = 1 cm.

Rib count. *Argonauta nouryi* shells are reported to have more ribs than *A. cornutus* shells: the ribs in *A. nouryi* are “more numerous” than in other species of *Argonauta*, while *A. cornutus* is reported to have “few radial ribs” (Voss, 1971, p. 32–33).

To investigate variation in the number of ribs per shell across the lot, RC was plotted against ShL (fig. 7). Probability plots indicate that both RC and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear

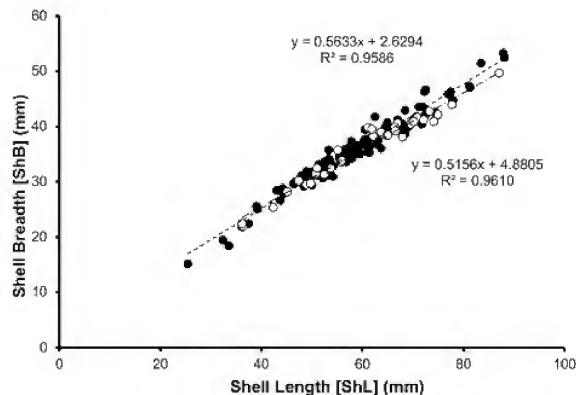


Figure 6. Variation in shell shape across the examined SBMNH lot. Scatter plot of shell breadth (ShB) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

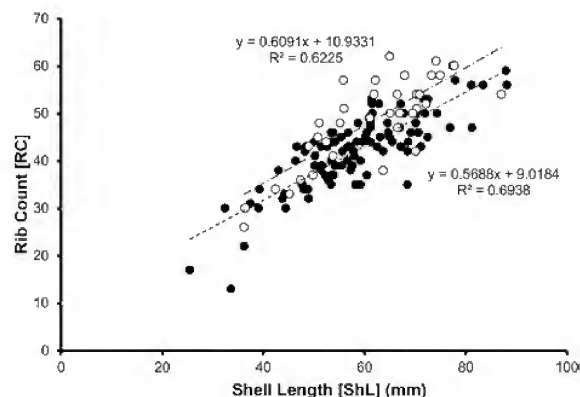


Figure 7. Variation in rib number across the examined SBMNH lot. Scatter plot of rib count (RC) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 3045766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, RC the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the number of ribs per shell does exist between eared and earless shells ($F_{(1, 136)} = 21.2$, $p < 0.001$).

Other features. To investigate the full range of quantifiable shell characters across the lot, scatter plots were similarly generated to investigate KTC, ApL, ApW and KW.

Keel tubercle count. To investigate variation in the number of keel tubercles per shell across the lot, KTC was plotted against ShL (fig. 8). Probability plots indicate that both KTC and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, KTC the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the number of keel tubercles per shell does exist between eared and earless shells ($F_{(1, 136)} = 51.66$, $p < 0.001$).

Aperture length. To investigate variation in the length of the shell apertures across the lot, ApL was plotted against ShL (fig. 9). Probability plots indicate that both ApL and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ApL the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the length of the aperture does exist between eared and earless shells ($F_{(1, 136)} = 18.63$, $p < 0.001$).

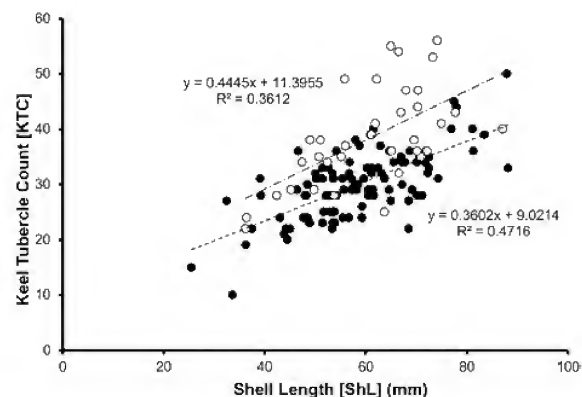


Figure 8. Variation in keel tubercle number across the examined SBMNH lot. Scatter plot of keel tubercle count (KTC) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Aperture width. To investigate variation in the width of the shell apertures across the lot, ApW was plotted against ShL (fig. 10). Probability plots indicate that both ApW and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ApW the

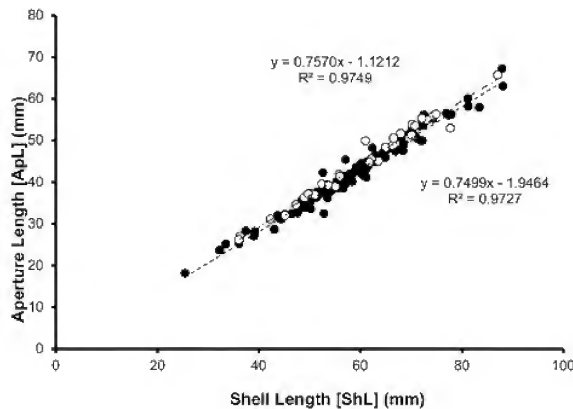


Figure 9. Variation in aperture length across the examined SBMNH lot. Scatter plot of aperture length (ApL) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

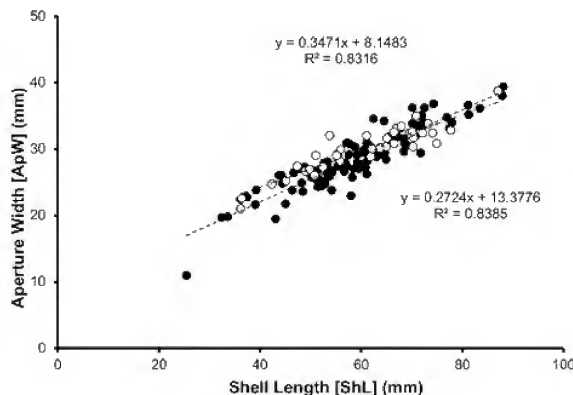


Figure 10. Variation in aperture width across the examined SBMNH lot. Scatter plots of aperture width (ApW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in the width of the aperture does exist between eared and earless shells ($F_{(1,136)} = 4.07$, $p = 0.046$).

Keel width. To investigate variation in the width of the shell keels across the lot, KW was plotted against ShL (fig. 11). Probability plots indicate that both KW and ShL follow normal distributions. An ANCOVA was used to determine if the slopes of the linear regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, KW the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are equal and hence a significant difference in the width of the keel does not exist between eared and earless shells ($F_{(1,136)} = 0.87$, $p = 0.353$).

Statistical analysis indicates that significance differences in shell dimensions was associated with the presence or absence of ears. Eared shells have significantly lower RC ($p < 0.001$), lower KTC ($p < 0.001$), shorter ApL ($p < 0.001$), increased ShB (i.e. shortened; $p = 0.02$) and increased ApW ($p = 0.046$). Earless shells have significantly higher RC ($p < 0.001$), higher KTC ($p < 0.001$), longer ApL ($p < 0.001$), reduced ShB (i.e. elongate; $p = 0.02$) and reduced ApW ($p = 0.046$). KW was found to not be significantly different between shell types ($p = 0.353$).

Historically, the features of eared and earless shell types have been considered to represent separate species such that features of eared shells are considered characteristic of *A. cornutus*, while features of earless shells are considered characteristic of *A. nouryi*.

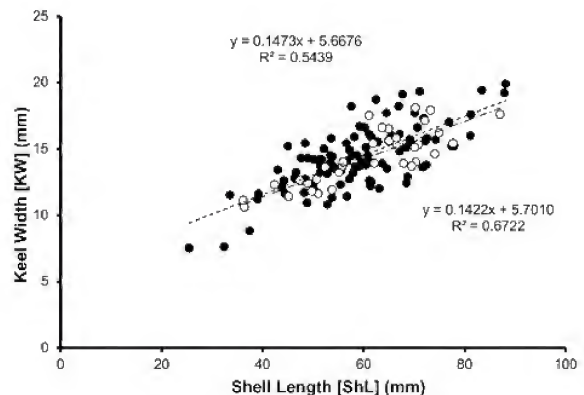


Figure 11. Variation in keel width across the examined SBMNH lot. Scatter plot of keel width (KW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Two types of shell formation

Close examination of individual shells revealed that features considered characteristic of each shell type could occur on a single shell. While individual shells could display features of both eared and earless shell types, the characters did not appear in isolation. Sequential growth sections of the shells appeared to display all the characteristics of one shell type or another. For example, the initial component of the shell (the smallest whorl) may display all the characters historically associated with an *A. cornutus* shell while the latter component (the larger final whorl) may display all the features associated with an *A. nouryi* shell.

The most dramatic examples were shells that appeared to have been repaired over the course of the argonaut's life. Fig. 12 presents photographs of one such shell from lot SBMNH 357476 (52.3 mm ShL). The initial component of the shell clearly displays the features historically attributed to *A. nouryi* (numerous fine ribs, reduced keel tubercles and no apparent ears), while the later component, following the clear repair line, displays a transition to features historically attributed to *A. cornutus* (ribs reduced in number and more pronounced, keel tubercles reduced in number and of larger size, and initiation of ears).

The presence of both shell types on a single shell clearly demonstrates that they represent different types of shell formation, not different argonaut species. This observation is supported by morphological evidence; despite full examination of nine female argonauts with shells (six historically identified as *A. cornutus* and three *A. nouryi*), no morphological characters could be found to separate specimens with different shell types (see Finn, 2013).

The realisation that the two shell morphs represented two shell formation types, not two argonaut species, required that they be defined independent of previous species association:

- Type 1 shell formation (historically attributed to *A. cornutus* shells) – formation of ears, few pronounced ribs, few large keel tubercles, appearance of more pronounced arch in the keel resulting in a tighter final whorl (i.e. increased ShB, reduced ApL).
- Type 2 shell formation (historically attributed to *A. nouryi* shells) – absence of ears, numerous less pronounced ribs, numerous small keel tubercles, appearance of less pronounced arch in the keel resulting in the appearance of a shallower final whorl and elliptical shell (i.e. reduced ShB, increased ApL).

An important character associated with Type 2 shell formation is inter-keel tuberculation (tubercles on the keel surface; see fig. 2e). The appearance of inter-keel tuberculation on the keel of a shell flags a shift to Type 2 shell formation, while a loss of inter-keel tuberculation signifies a shift to Type 1 shell formation.

Based on this realisation, it became clear that this large lot, and all other material examined of these shell morphs, belonged to a single species. Because *A. nouryi* Lorois, 1852, has date priority over *A. cornutus* Conrad, 1854; this study treats *A. nouryi* as the available name. See Finn (2013) for full synonymy.

The key to understanding shell variation

The realisation that individual shells may be composed of combinations of two types of shell formation provided the key to understanding the huge variation in shell shape across the single large collection of argonaut shells from Baja California. Combinations of sequential shell formation could be recognised in all shells and hence their varied appearance could be understood. Shells were recognised within this single lot that display a single type of shell formation plus those with one, two or three transformations between the two shell formation types.

The initial whorl of most of the shells displayed Type 1 formation. Shell #37 displays a single change from Type 1 to Type 2 shell formation (fig. 13). Shell #72 displays a change from Type 1 to Type 2 shell formation and then a change back to Type 1 (fig. 14). Shell #41 displays a change from Type 1 to Type 2 shell formation and then a change back to Type 1 and then to Type 2 (fig. 15). Damage to shells normally results in a conversion to Type 2 shell formation.

In a transition between shell formation types, ears may be formed or subsumed. This is displayed across many shells within the lot. For examples, shell #139 displays subsumed ears as a result of a transition from Type 1 to Type 2 shell formation (fig. 16), while shell #136 displays ear formation, separate from the axis of the shell, as a result of a transition from Type 2 to Type 1 shell formation (fig. 17).

Type material. Available type material for additional species synonymised with *A. nouryi* Lorois, 1852, was also examined for shifts in shell formation type. The holotype of *A. dispar* Conrad, 1854 (54.9 mm ShL, ANSP 129978) displays a single change from Type 2 to Type 1 shell formation (fig. 18). The holotype of *A. expansus* Dall, 1872 (80.2 mm ShL [P], USNM 61368), displays two changes – from Type 1 to Type 2 and then back to Type 1 (fig. 19).

Shell thickness. Preliminary observations suggested that the shell walls of Type 1 formation are thicker than the walls of Type 2 formation. To investigate this phenomenon, a scanning electron microscope was used to examine variation in shell thickness across recognisable shell breaks that corresponded with a switch between shell types (a single damaged shell from lot SBMNH 357476 was sacrificed). Preliminary results indicate a reduction in shell wall thickness between Type 1 and Type 2 formation. Fig. 20 presents two scanning electron micrographs displaying a reduction in thickness across a break signifying transition from Type 1 to Type 2. Shell thickness on the lateral face drops from approximately 220 to 140 μm (fig. 20a), while thickness at the keel drops from approximately 275 to 210 μm in this shell (fig. 20b).

A lack of material that could be fragmented for examination with a scanning electron microscope limited the extent to which this phenomenon could be investigated. The lots housed in the SBMNH collection are too valuable to be considered for this style of destructive investigation.

A reduction in shell wall thickness may be related to producing a larger shell area with less shell material. The resulting thinner walled shell (Type 2) would therefore consist

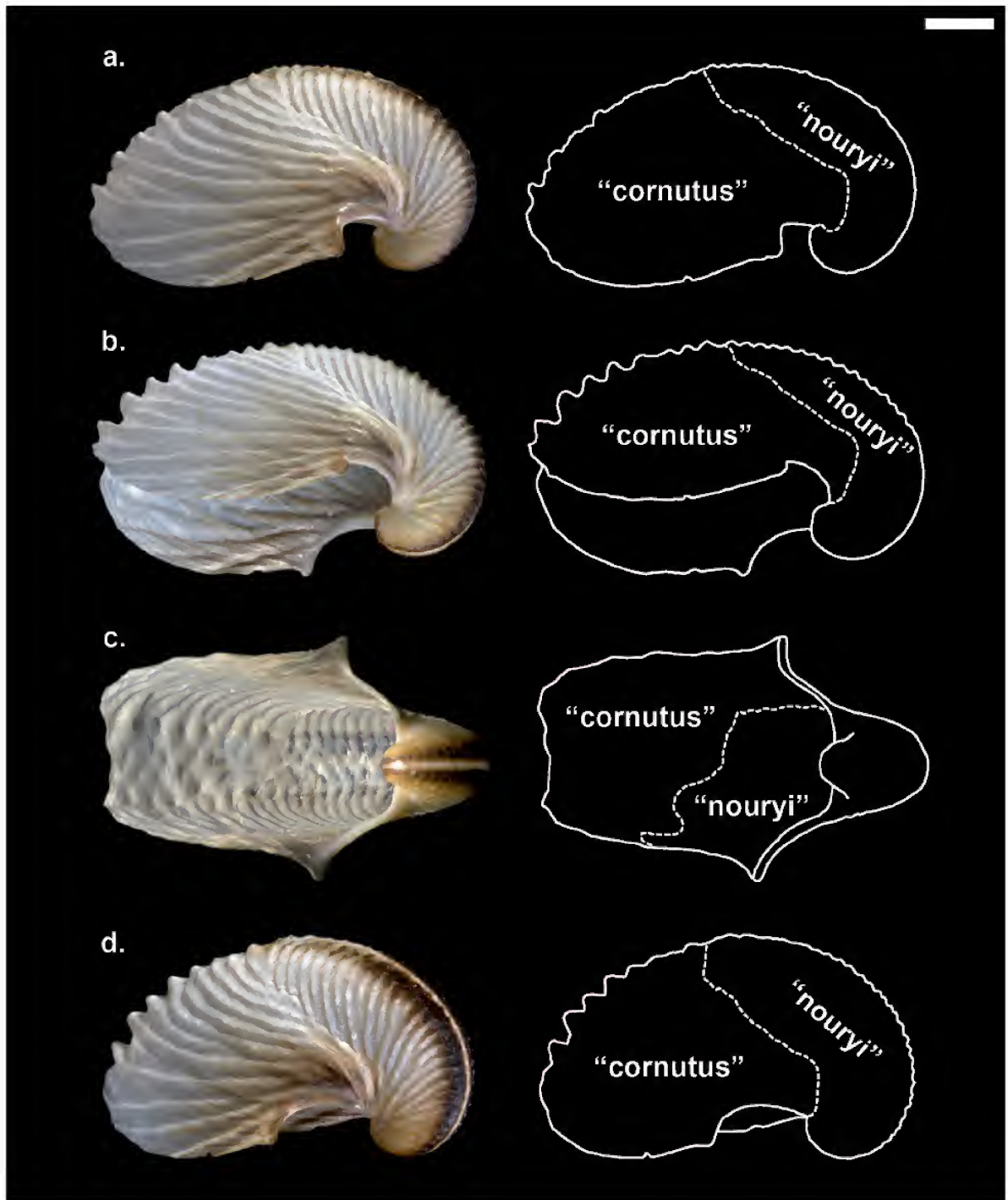


Figure 12. Repaired shell displaying components consistent with *Argonauta nouryi* and *A. cornutus*: a–d, four perspectives of a single shell (52.3 mm shell length, SBMNH 357476) displaying an initial component consistent with *A. nouryi* Lorois, 1854 ("nouryi") followed by a subsequent component consistent with *A. cornutus* Conrad, 1854 ("cornutus"); a, right lateral view; b, oblique right lateral view; c, anterior aperture view; d, oblique ventral keel view. Dashed line represents repair line separating two visually different components. Scale bar = 1 cm.

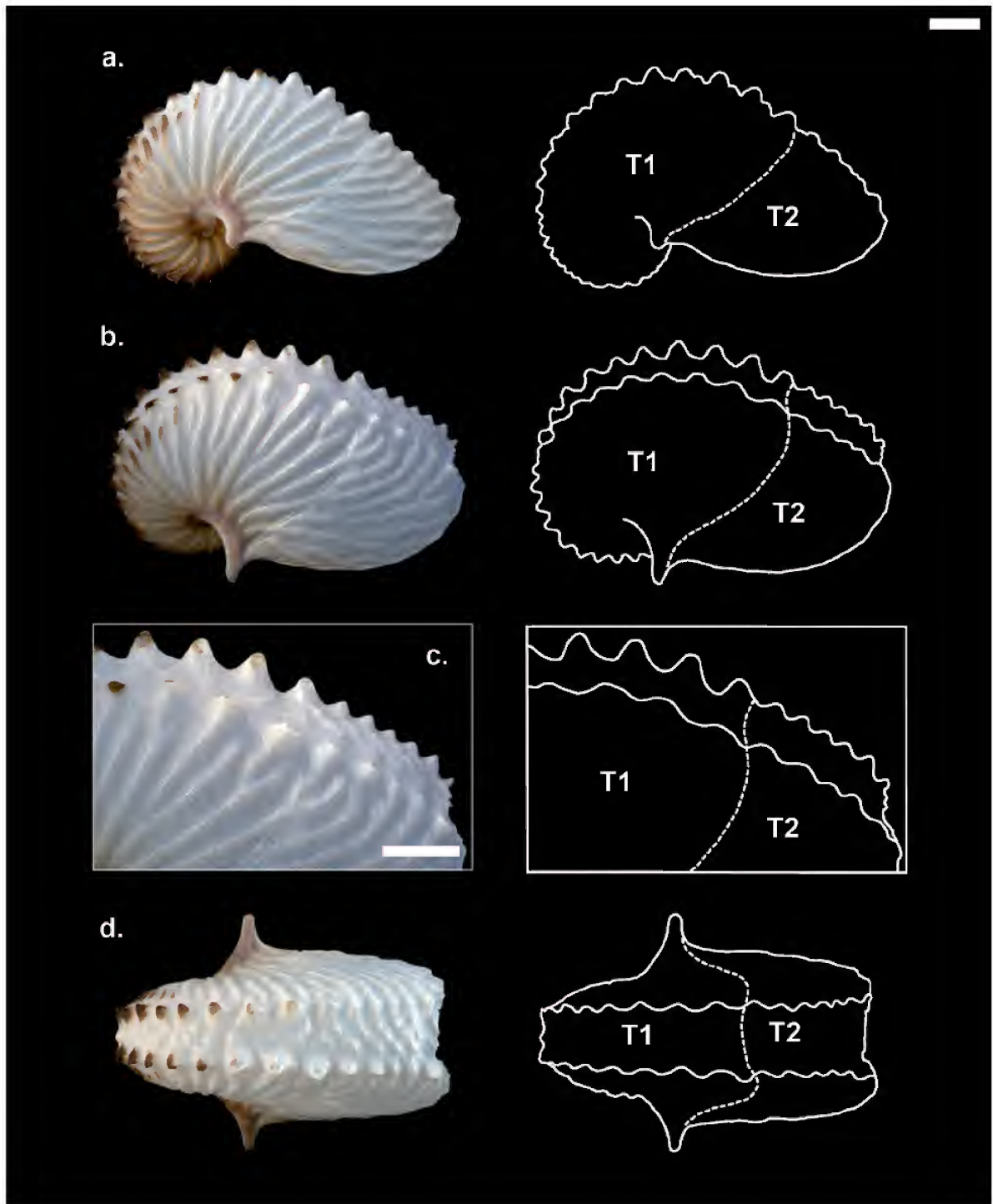


Figure 13. *Argonauta nouryi* shell displaying a single change in shell formation type: a–d, four perspectives of shell #37 (65.5 mm shell length, SBMNH 345766) displaying a single change from Type 1 (T1) to Type 2 (T2) shell formation; a, left lateral view; b, oblique left lateral view; c, close-up oblique left lateral view; d, posterior keel view. Scale bar = 1 cm.

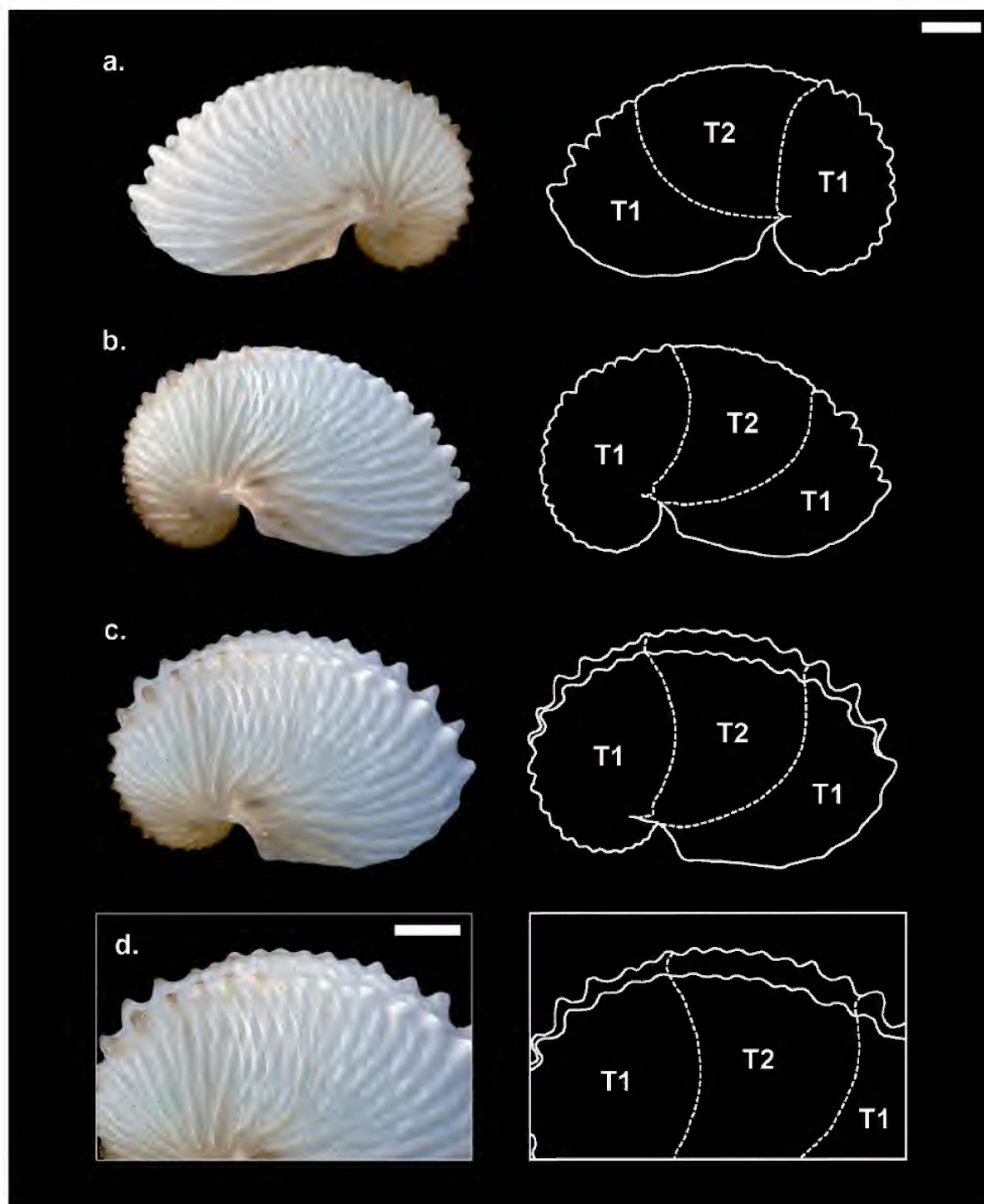


Figure 14. *Argonauta nouryi* shell displaying two changes in shell formation type: a–d, four perspectives of shell #72 (55.4 mm shell length, SBMNH 345766) displaying two changes from Type 1 (T1) to Type 2 (T2) shell formation and back to Type 1; a, right lateral view; b, left lateral view; c, oblique left lateral view; d, close-up oblique left lateral view. Scale bar = 1 cm.

of less calcium carbonate and weigh less than an equivalently sized thicker walled shell (Type 1). The relative weights of the three shells presented in fig. 5 appear to support this theory. The Type 1 shell (*cornutus*-type voucher; 4.0 g) is 1.3 times the weight of the Type 1/Type 2 shell (*intermediate* voucher; 3.1 g) and 1.7 times the weight of the Type 2 shell (*nouryi*-type voucher; 2.4 g), despite the shells having similar ShL. Weight (g) to length (mm) ratios of the three shells were: 1:16 for the Type 1 shell (*cornutus*-type voucher); 1:20 for the Type 1/Type 2 shell (*intermediate* voucher); 1:28 for the Type 2 shell (*nouryi*-type voucher). These ratios suggest that per gram of calcium carbonate, Type 2 shell production results in a shell 1.8 times the length of a Type 1 shell.

To investigate this relationship across the lot, ShW was plotted against ShL with eared and earless shells distinguished (fig. 21). The scatter plot indicates a separation between eared and earless shells based on weight. This difference was analysed statistically to determine significance. Probability plots indicate that both ShW and ShL follow normal distributions. An ANCOVA was used to determine if the

slopes of the regression lines, generated for eared and earless shells, were the same or different. Shell type (eared or earless) was the independent variable, ShW the dependent variable and ShL the covariate. The ANCOVA revealed that the slopes of the regression lines are not equal and hence a significant difference in weight exists between eared and earless shells ($F_{(1, 136)} = 86.7, p < 0.001$).

Argonauta hians [Lightfoot], 1786; the *A. hians/boettgeri* complex

Recognition of shell form transformations in *A. nouryi* provided a new perspective on shell variation in another highly variable group of small argonauts, the *A. hians/boettgeri* complex.

The original description of *A. hians* [Lightfoot], 1786, refers to a single image in Rumphius (1705): plate 18, figure B (fig. 22a), designated as a lectotype by Moolenbeek (2008) in the absence of type material. Shells of *A. hians* can be recognised by smooth lateral ribs and a keel that increases in width with shell growth. Inter-keel tuberculation is absent.

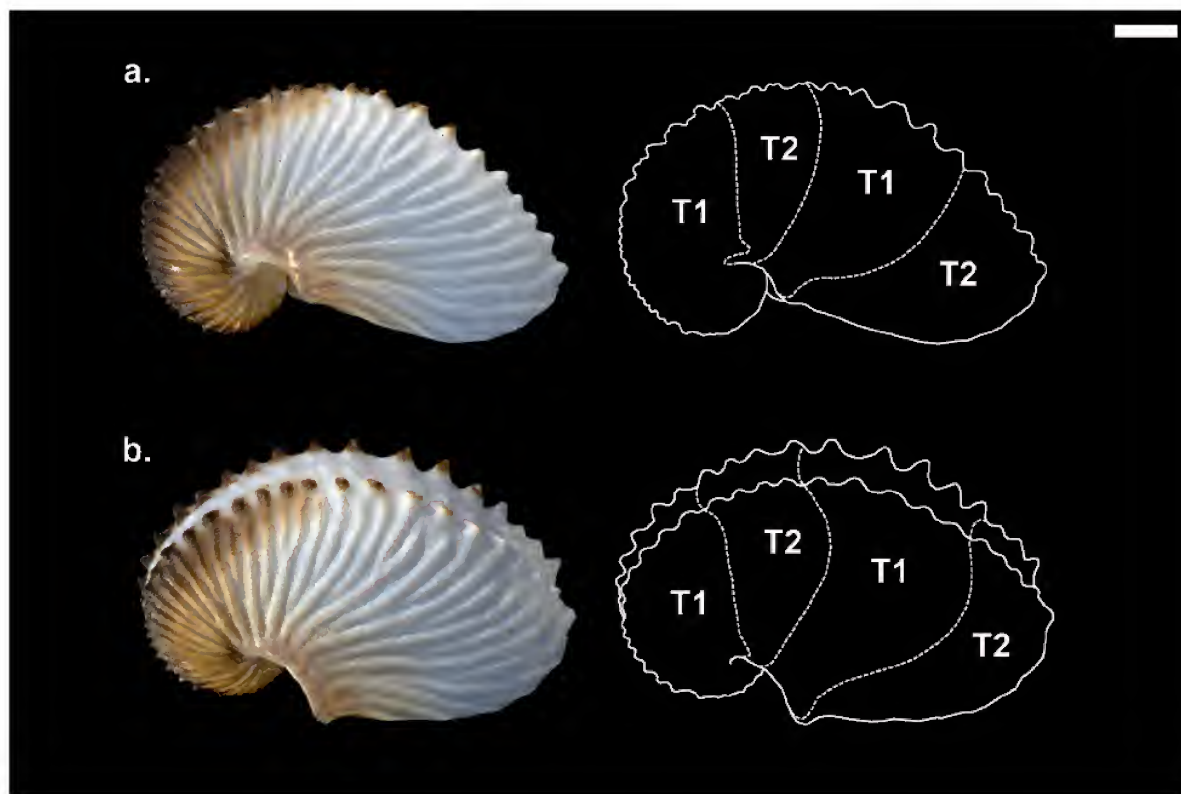


Figure 15. *Argonauta nouryi* shell displaying three changes in shell formation type: a–b, two perspectives of shell #41 (64.7 mm shell length, SBMNH 345766) displaying three changes in shell formation type from Type 1 (T1) to Type 2 (T2) shell formation, back to Type 1 and then to Type 2; a, left lateral view; b, oblique left lateral view. Note that the key to recognising the different shell formation types (challenging in this shell) is to look for reductions in the size of sequential keel tubercles (that would normally increase in size), a change in the relative distance between keel tubercles, a change in the ratio of lateral ribs to keel tubercles, and the appearance or disappearance of inter-keel tuberculation. Scale bar = 1 cm.

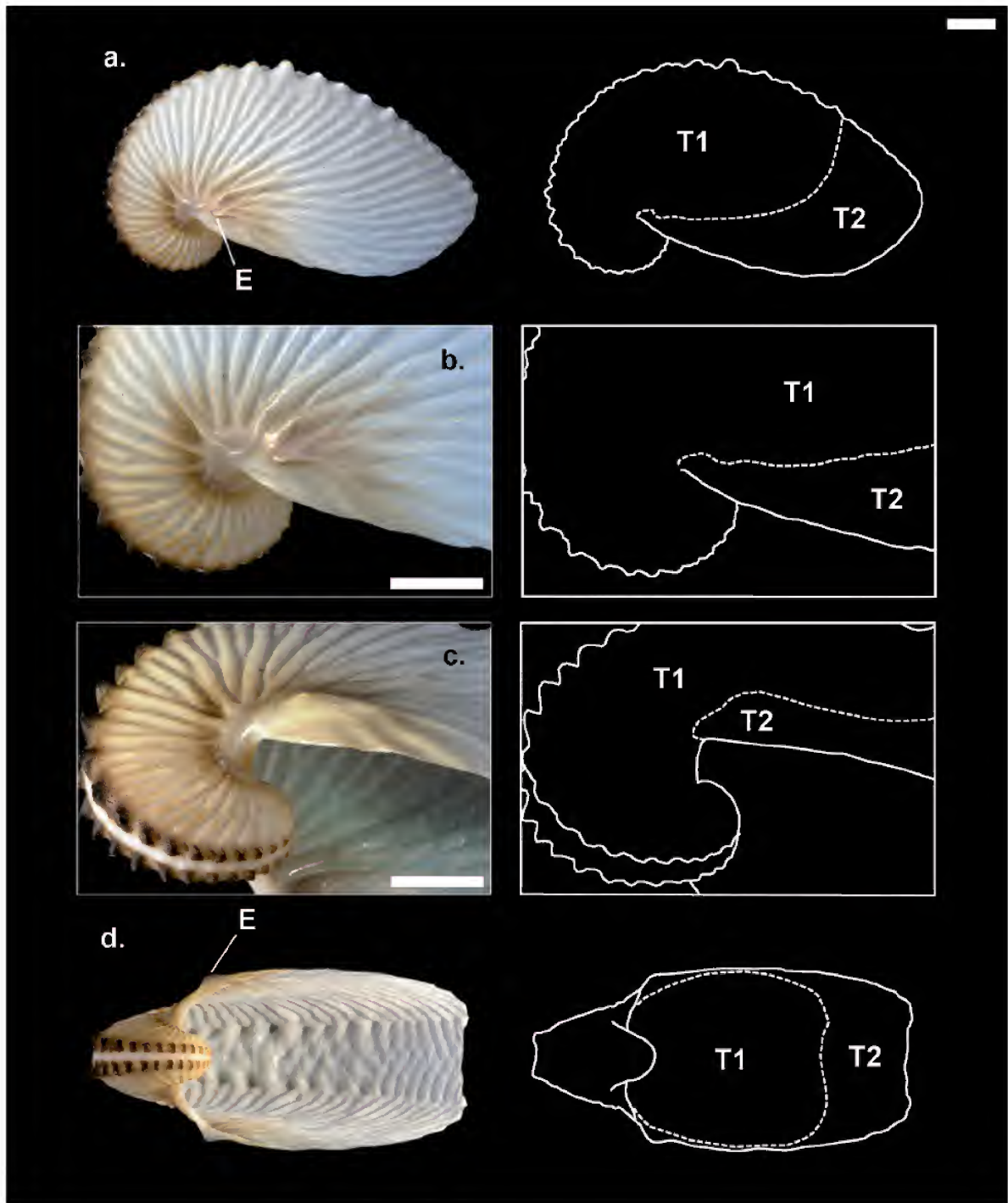


Figure 16. *Argonauta nouryi* shell displaying subsumed ears: a–d, four perspectives of shell #139 (72.2 mm shell length, SBMNH 345768) displaying subsumed ear (E) associated with a shift from Type 1 (T1) to Type 2 (T2) shell formation; a, left lateral view; b, close-up of subsumed ear, left lateral view; c, close-up of subsumed ear, oblique left lateral view; d, anterior aperture view. The shell added to the aperture edge in Type 2 shell formation does not expand the ear, instead subsuming it. The resulting aperture edge is not eared. Scale bars = 1 cm.

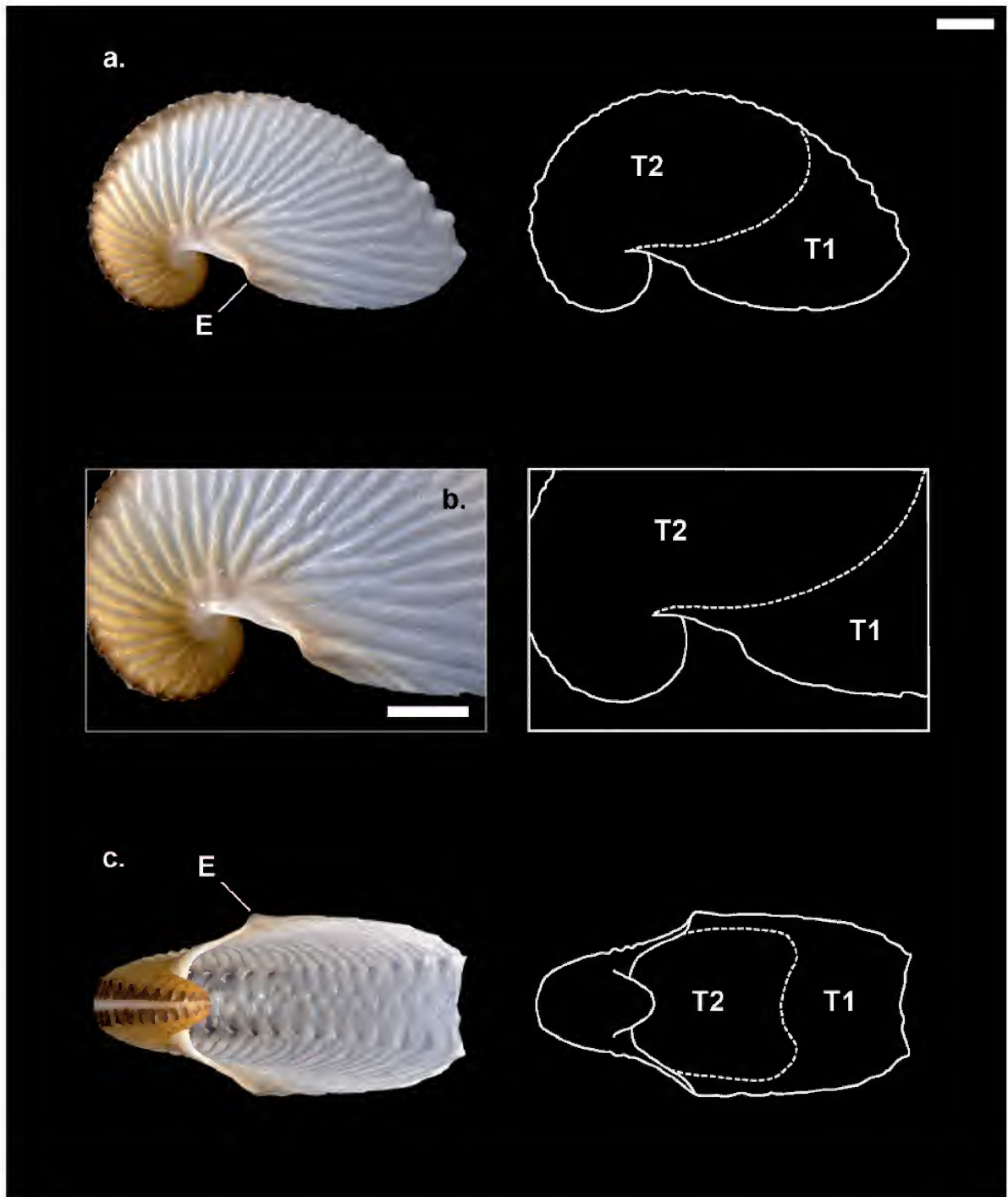


Figure 17. *Argonauta nouryi* shell displaying ear formation: a–c, three perspectives of shell #136 (63.1 mm shell length, SBMNH 345768) displaying ear (E) formation associated with a shift from Type 2 (T2) to Type 1 (T1) shell formation; a, left lateral view; b, close-up of ear, left lateral view; c, anterior aperture view. The shell added to the aperture edge in Type 1 shell formation produces a new ear separate from the axis of the shell. The new ear becomes the widest point on the aperture edge. Scale bars = 1 cm.

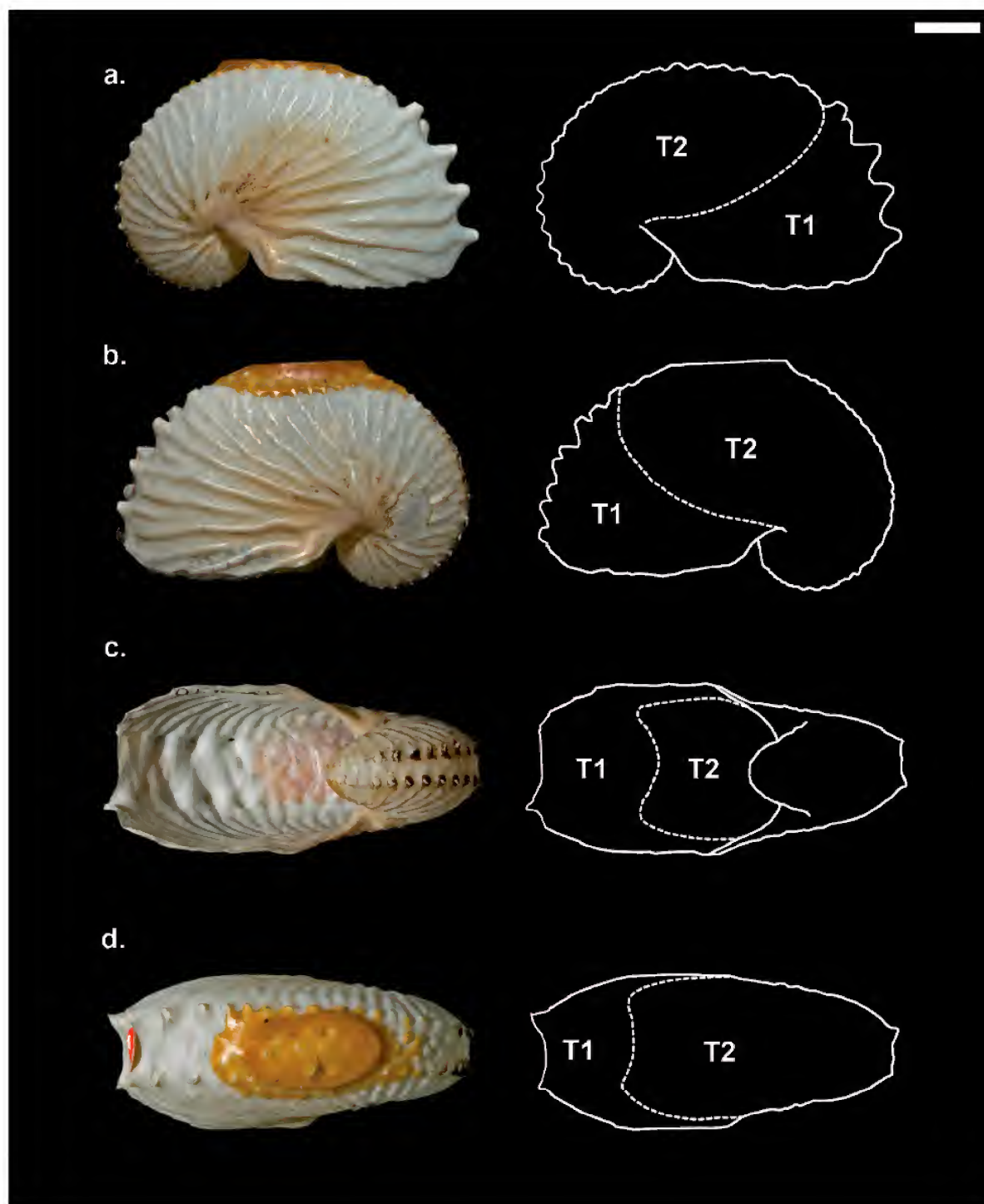


Figure 18. Holotype of *Argonauta dispar* Conrad, 1854 (synonym of *A. nouryi* Lorois, 1852) from the Academy of Natural Sciences, Philadelphia: a–d, four perspectives of *A. dispar* Conrad, 1854 Holotype (54.9 mm shell length, ANSP 129978) displaying a single change from Type 2 (T2) to Type 1 (T1) shell formation; a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

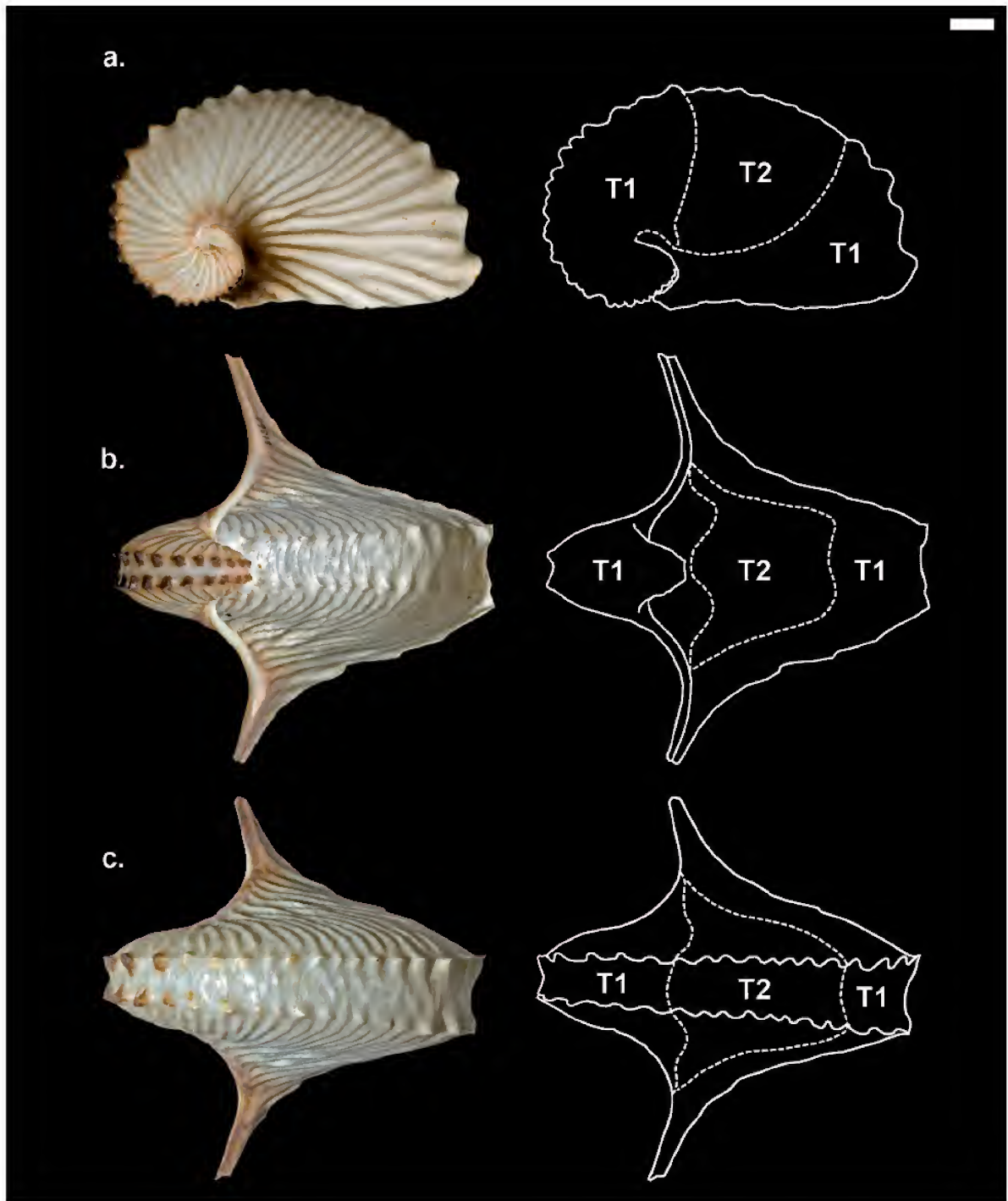


Figure 19. Holotype of *Argonauta expansus* Dall, 1872 (synonym of *A. nouryi* Lorois, 1852) from the National Museum of Natural History (Smithsonian Institution) Washington: a–c, three perspectives of *A. expansus* Dall, 1872 Holotype (80.2 mm shell length [P], USNM 61368) displaying two changes from Type 1 (T1) to Type 2 (T2) shell formation and back to Type 1; a, left lateral view; b, anterior aperture view; c, posterior keel view. Scale bar = 1 cm.

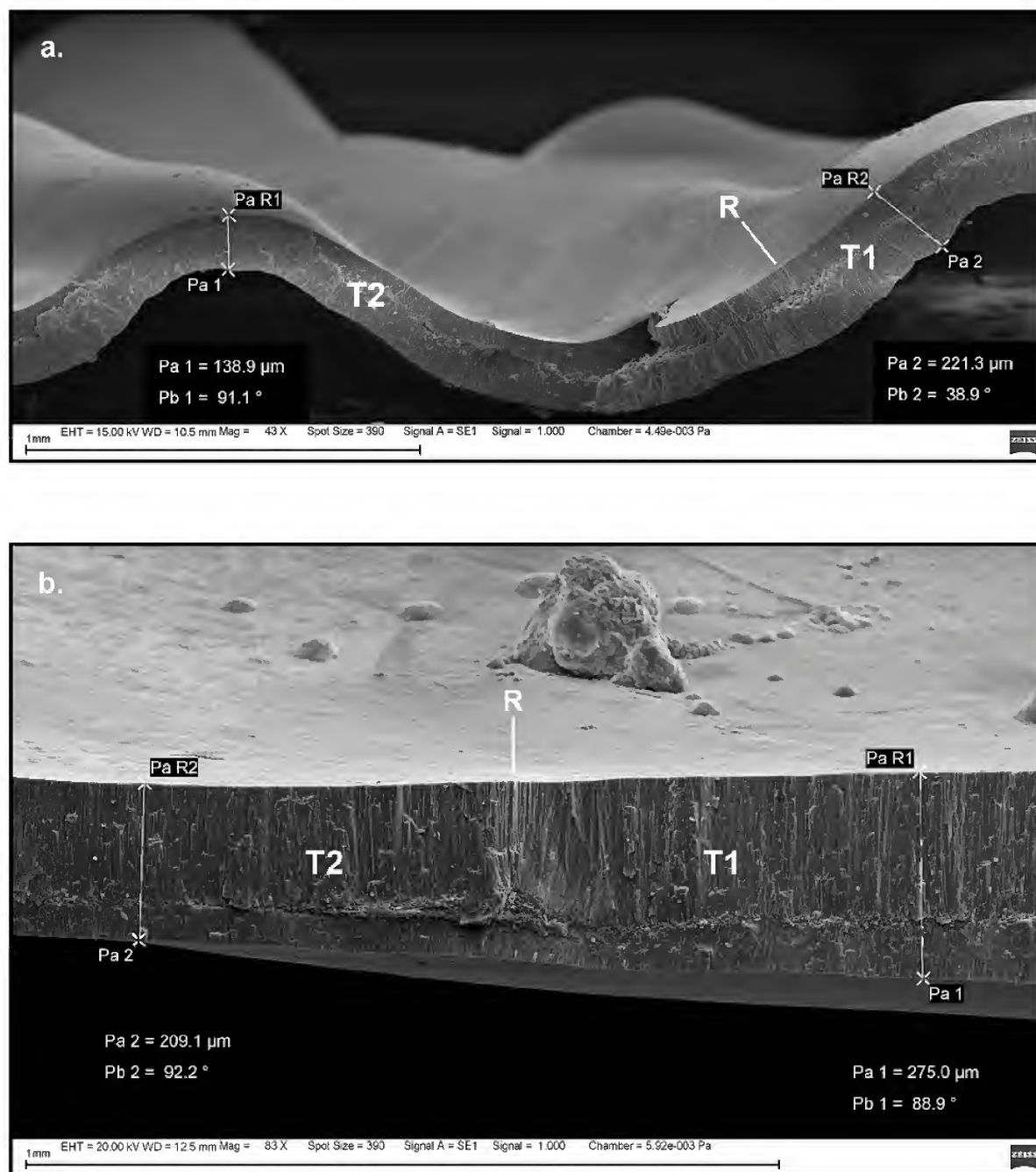


Figure 20. Scanning electron microscope images of *Argonauta nouryi* shell displaying variation in shell thickness: a–b, scanning electron microscope images of shell cross-sections (SBMNH 357476) across shell repairs (R) representing a shift from Type 1 (T1) to Type 2 (T2) shell formation; a, lateral face of shell, inner surface facing up; b, keel, outer surface facing up. Scale bars = 1 mm.

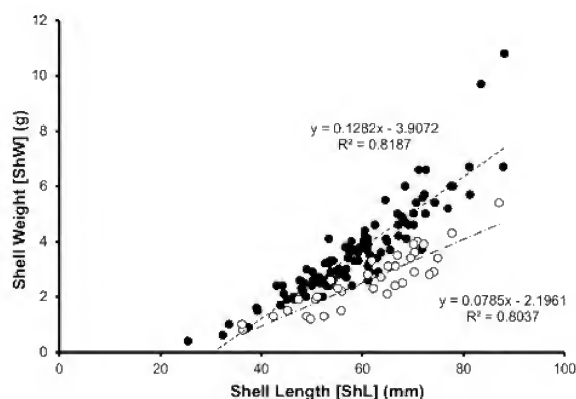


Figure 21. Variation in shell weight across the examined SBMNH lot. Scatter plot of shell weight (ShW) against shell length (ShL) for the single shell lot collected at El Mogote, La Paz, Baja California Sur, Mexico (24° 10' 00" N, 110° 24' 00" W) on 15 January 2000 (SBMNH 345766 & 345768). Eared shells (solid circles) and earless shells (open circles) distinguished. Linear regression lines for eared shells (dashed) and earless shells (dot dashed) with corresponding equations and coefficients of determination (i.e. R^2 values) presented.

Argonauta hians has long been recognised as displaying considerable variation in shell form. Voss and Williamson (1971) noted that “In the series from Hong Kong the sides of the aperture at the umbilicus range from strongly eared or auriculate with very large few knobs on the keel to specimens with no trace of auriculation and with rather more numerous, smaller knobs” (p. 105). They found that “if the 30 shells are laid out graded from large few knobs and strong auricles to smaller, more numerous knobs and flat sides there is an even gradation with no breaks or sudden changes” (p. 105). They concluded that all shells “belong to the same species” (p. 105).

As part of this study, 274 *A. hians* shells were directly examined in museum and private collections in Australia, United States, Europe, South Africa and Japan. With knowledge gained from examining shells of *A. nouryi*, all shells from all sites were examined for an abrupt change in keel tubercle height or ears that had been formed or subsumed in single shells. Because inter-keel tuberculation is not expressed in argonaut shells other than *A. nouryi*, this character could not be used.

Two shell formation types. Shells of *A. hians* were found to display two clear shell formation types:

- Type 1 shell formation – few pronounced ribs, large prominent keel tubercles, formation of ears.
- Type 2 shell formation – numerous less-pronounced ribs, small and greatly reduced, keel tubercles, absence of ears.

These shell formation types are similar to those expressed in *A. nouryi* except that variation in the arch of the shell was not observed and inter-keel tuberculation was not present.

This variation had been noted by Voss and Williamson (1971) who stated: “The knobs on the keel are very large and

prominent in the first half of the shell and may remain large on the last half or may become considerably smaller” (p. 105).

Two shells are presented as examples:

- A shell from the Philippines (79.6 mm ShL [P], BMNH unreg., “Cuming, i.”) (fig. 23). This shell displays a clear shift from Type 1 to Type 2 shell formation indicated by a reduction in the size and spacing of the keel tubercles, a reduction in the ratio of ribs to keel tubercles from approximately 1.5:1 to 1:1 and ears subsumed.
- A shell from the North West Shelf, Western Australia (53.0 mm ShL, WAM S31510) (fig. 24). This shell displays a shift from Type 1 to Type 2 shell formation. This transition occurred when the shell was at a smaller size and hence the ears are less developed. The resultant aperture shape (fig. 24c) is extremely similar to that observed in Type 2 *A. nouryi* shells; see fig. 5c, ii for comparison.

Variation also occurs between the opposing faces of individual shells, further highlighting the plasticity of shell characters in this species. A single shell is presented here as an example:

- A shell from Madagascar (60.8 mm ShL, NMV F164734, “Madagascar”) displays a large ear on the right side only; the left side is earless (fig. 25).

The *A. hians*/boettgeri complex. Small, earless *A. hians* shells have regularly been attributed to the species *A. boettgeri* Maltzan, 1881 (fig. 22b, c). Smith (1887) outlined the diagnostic characters of *A. boettgeri*: “The distinguishing features of this species are the numerous ribs and tubercles, the total absence of auricular expansions at the sides, its constantly small size, and the fine granulation (a feature not remarked upon by Maltzan), which more or less covers the whole surface, producing a dull non-glossy appearance” (p. 409). Berry (1914) similarly noted that the shell of *A. boettgeri* “seems unique in its small size, compact coil, and the circumstance that the auricular expansion at the sides of the aperture, so frequently developed in other species of the genus, are here notable only for their entire absence” (p. 280). Robson (1932) added “the almost invariable absence of colouring on the carinal knobs” to the distinguishing characters of *A. boettgeri* (p. 197). While Smith (1887) concludes that “the shell of this species must not be confounded with young stages of *A. hians*; the more numerous ribs and tubercles and the rougher granular surface will separate it” (p. 410). Unfortunately, this dichotomy is not so straightforward.

Of the 274 *A. hians* shells examined, 41 can be attributed to *A. boettgeri* based on the above description. While it is possible to select a subset of shells possessing these characteristics, which in isolation appear distinct, examination of the entire range of material quickly dissolves the parameters on which this subset is based. All features mentioned above are variable in *A. hians*: ribs and keel tubercles can be numerous or scarce, pronounced or reduced, consistent across the shell or variable; ears can be present or absent, produced or subsumed, expressed on one side of the shell or both; the shell surface can be granular or smooth, pigmented or white. Two shells, displaying variation across the growth of the shell, are presented as examples:

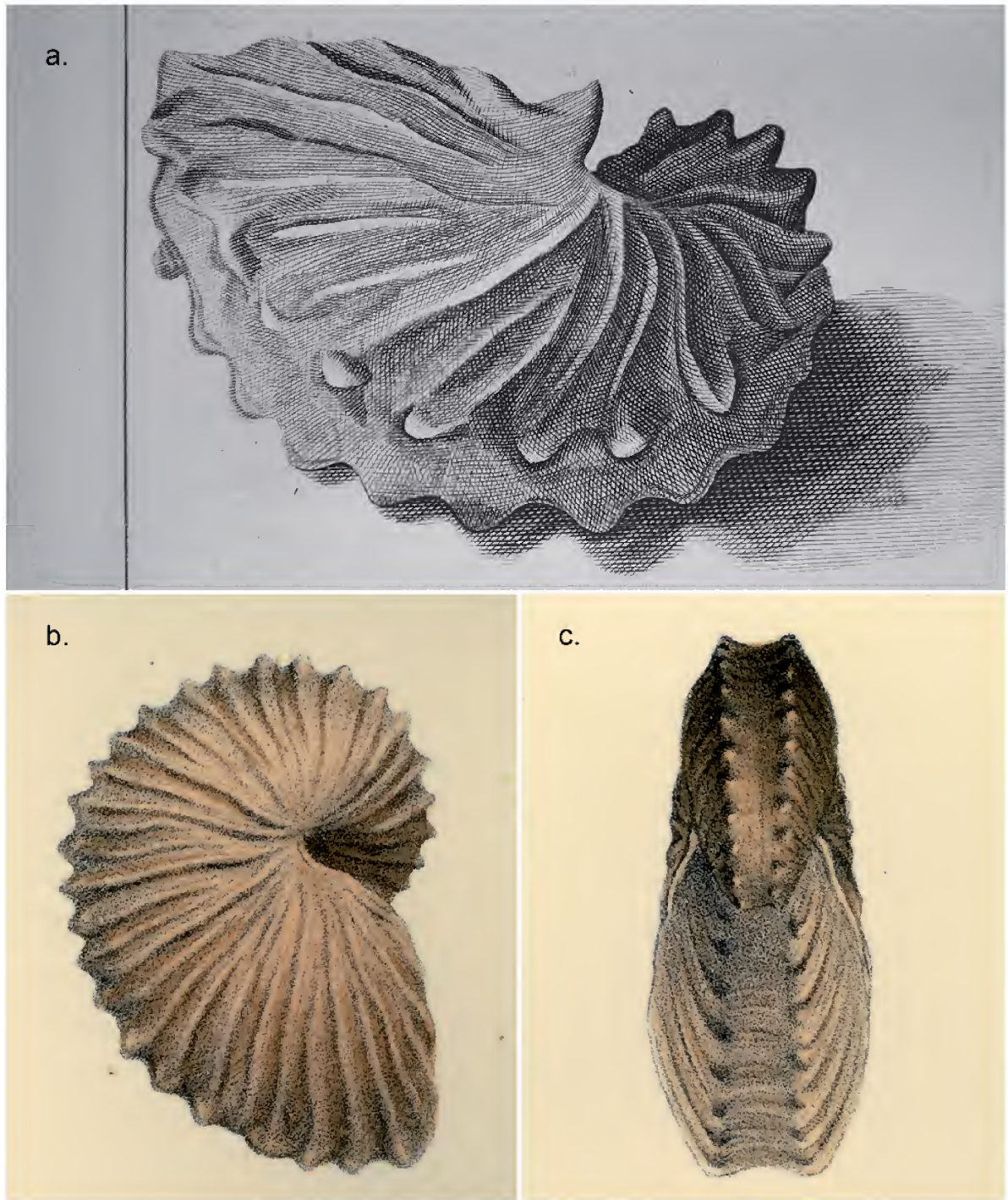


Figure 22. Reproduced illustrations referenced in the descriptions of *Argonauta hians* [Lightfoot], 1786 and *A. boettgeri* Maltzan, 1882: a, illustration of *A. hians* [Lightfoot], 1786, designated as a lectotype by Moolenbeek (2008), Rumphius, 1705: pl. 18, fig. B; b–c, illustrations of *A. boettgeri* Maltzan, 1881, featured in the original publication, Maltzan, 1881: 163, pl. 6 fig. 7; b, right lateral view; c, anterior aperture view.

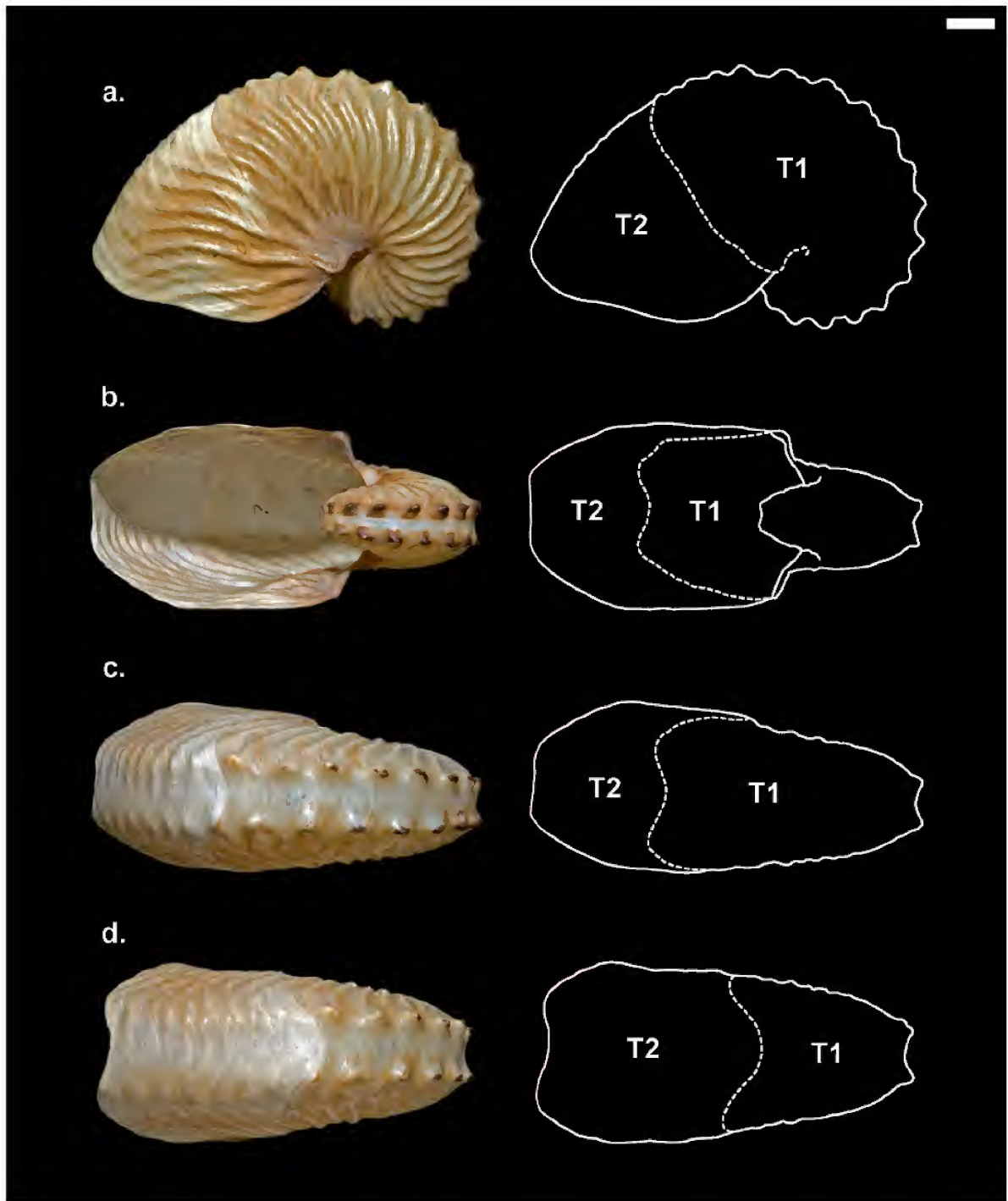


Figure 23. *Argonauta hians* shell from the Philippines: a–d, four perspectives of an *A. hians* shell from the Philippines (79.6 mm shell length [P], BMNH unreg., "Cuming, i.") displaying a clear shift from Type 1 shell formation (T1) to Type 2 shell formation (T2) indicated by a reduction in the size and spacing of the keel tubercles, a reduction in the ratio of ribs to keel tubercles (from approximately 1.5:1 to 1:1) and subsumed ears; a, right lateral view; b, anterior aperture view; c, posterior keel view; d, ventro-posterior keel view. Scale bar = 1 cm.

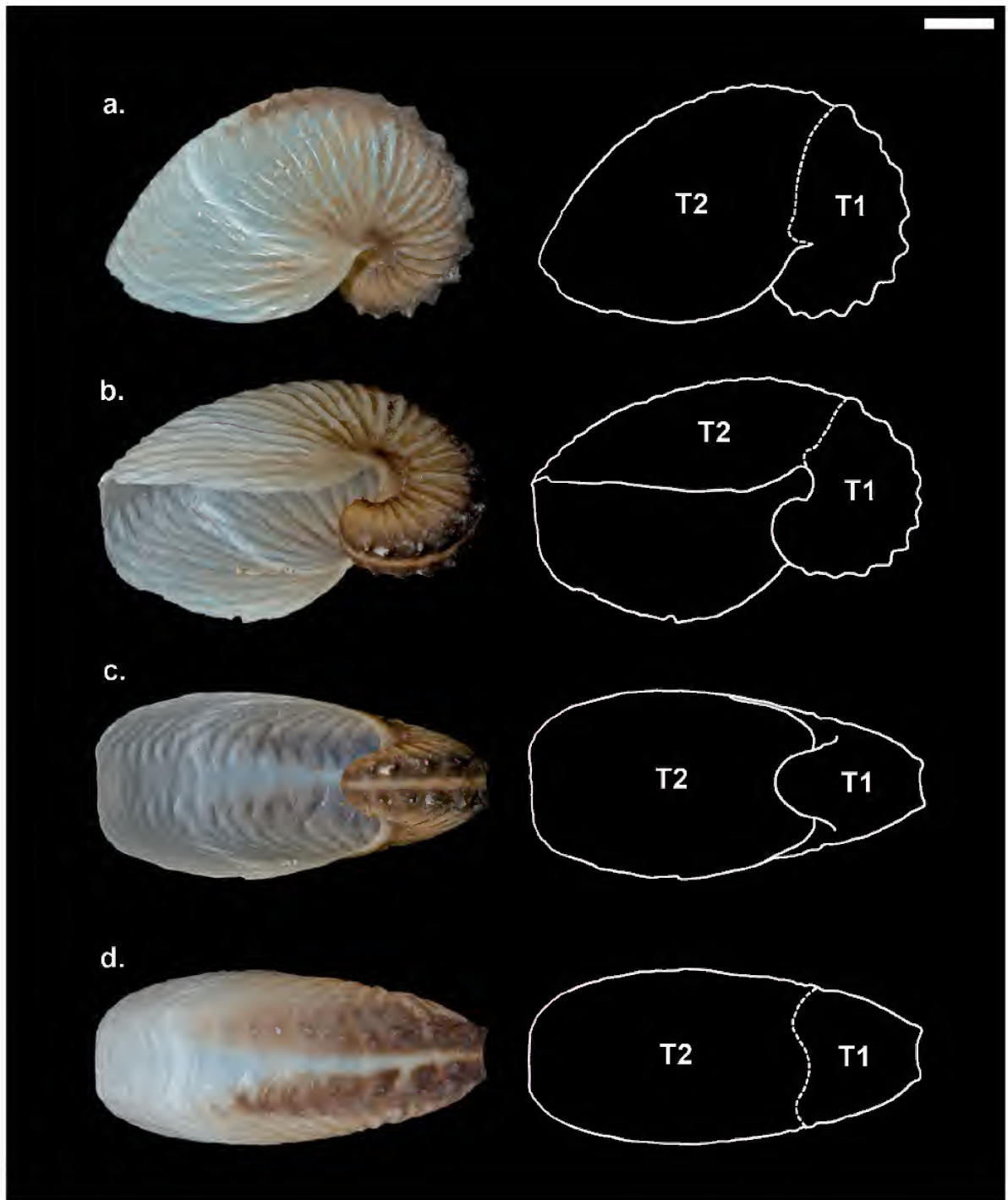


Figure 24. *Argonauta hians* shell from the North West Shelf, Western Australia: a–d, four perspectives of an *A. hians* shell from the North West Shelf, Western Australia (53.0 mm shell length, WAM S31510) displaying a clear shift from Type 1 shell formation (T1) to Type 2 formation (T2) indicated by a reduction in the size and spacing of the keel tubercles and a reduction in the ratio of ribs to keel tubercles (from approximately 1.5:1 to 1:1); a, right lateral view; b, oblique right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

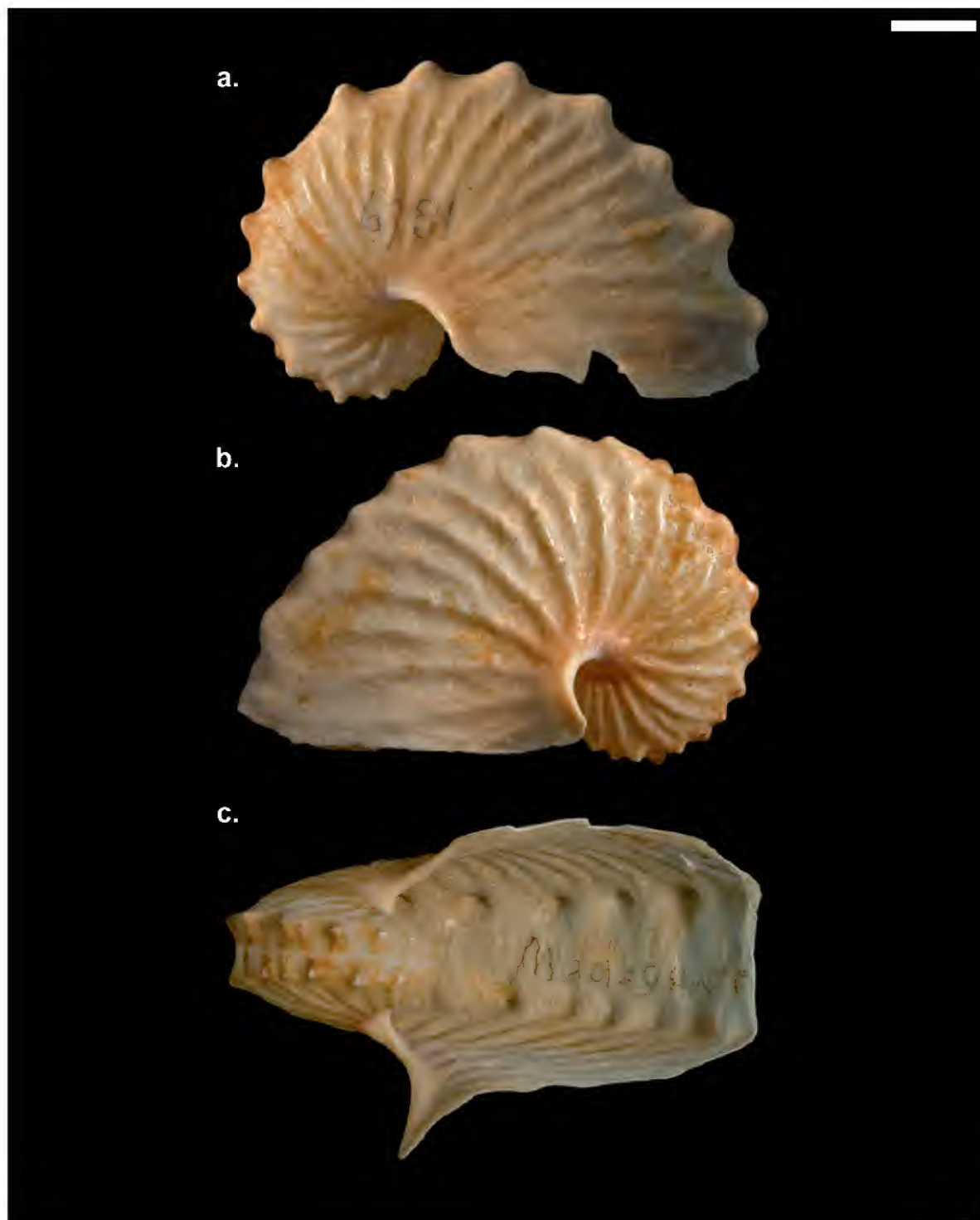


Figure 25. Single eared *Argonauta hians* shell from Madagascar: a–c, three perspectives of a single eared *A. hians* shell from Madagascar (60.8 mm shell length, NMV F164734); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

- A shell from the British Museum (76.1 mm ShL [P], BMNH unreg., locality unknown, “B698, t.”; fig. 26). This shell displays an aperture shape and axial region consistent with the original description of *A. boettgeri* (fig. 22b, c) yet defies the description of *A. boettgeri* by showing signs of possessing ears at an earlier growth stage. While the ears have been subsumed with a shift from Type 1 to Type 2 shell formation, only the keel tubercles on the right side show a reduction in size (fig. 26b); the left keel tubercles have remained large (fig. 26a).
- A shell from Museums Victoria (25.0 mm ShL [P], NMV F164767, locality unknown; fig. 27). This shell would historically have been attributed to *A. boettgeri* due to its small size and distinctive earless aperture. This shell displays a dramatic change in keel tubercle size and spacing associated with a shift from Type 2 to Type 1 shell formation, thus highlighting the plasticity of these characters.

In the absence of any consistent and definable diagnostic shell characters (in combination with a lack of diagnostic morphological characters or distinct distributions; see Finn, 2013), no evidence exists to justify maintaining *A. boettgeri* as a separate species. Consequently *A. boettgeri* Maltzan, 1881, is treated here as a synonym of *A. hians* [Lightfoot], 1786.

Insight from whole animals. As described in the Materials and Methods section above, a single specimen lot of 73 female *A. hians*, most with intact shells, exist in the collections of the

Western Australian Museum and Museums Victoria. On initial examination, it was found that the lot included submature, mature and spawned (i.e. females with eggs attached to the central axis of the shell) individuals. The shells of the spawned females tended to show a shift to Type 2 shell production in the last components of the shells (all other shells were composed entirely of Type 1 shell production). This led to the consideration that shell shape and transformation may be triggered by changes in reproductive stage or condition.

To understand the underlying cause of a change in shell formation type at the point of egg laying, a subset of 33 intact and measurable individuals were selected and fully measured. The subset included submature, mature and spawned individuals, with a size range of 13–27 mm DML and 21–36 mm ShL. Two larger females, also collected over the North West Shelf, were incorporated into the analysis to expand the size range (QM Mo77789: 39.9 mm DML and 51.8 mm ShL; 28.7 mm DML and 38.9 mm ShL).

Changes in shell morphometrics relative to animal size. Shell dimensions were plotted against DML to determine if the size of the shell relative to the size of the female changes between submature, mature and spawned individuals. Scatterplots against DML were generated for ShL, ShB, ApL, ApW, KW and EW. The scatter plots indicate a linear relationship between shell dimensions and animal size, with linear regressions returning coefficient of determination values (i.e. R^2 values) between 0.72 and 0.90 (see Table 1). No discontinuities were observed between the three maturity stages.

Table 1. Linear regression equations for scatter plots of shell dimensions (y) against dorsal mantle length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R^2 values) presented.

y	x	equation	R^2
Shell length (ShL)	Dorsal mantle length (DML)	$y = 1.0936x + 7.9242$	0.8980
Shell breadth (ShB)	Dorsal mantle length (DML)	$y = 0.8705x + 0.6315$	0.8705
Aperture length (ApL)	Dorsal mantle length (DML)	$y = 0.8889x + 3.4049$	0.8882
Aperture width (ApW)	Dorsal mantle length (DML)	$y = 0.3875x + 9.3432$	0.7697
Keel width (KW)	Dorsal mantle length (DML)	$y = 0.1839x + 4.1154$	0.7244
Ear width (EW)	Dorsal mantle length (DML)	$y = 0.3360x + 11.1327$	0.7268

Table 2. Linear regression equations for scatter plots of female argonaut dimensions (y) against dorsal mantle length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R^2 values) presented.

y	x	equation	R^2
Mantle width (MW)	Dorsal mantle length (DML)	$y = 0.4166x + 6.6124$	0.8156
Head width (HW)	Dorsal mantle length (DML)	$y = 0.4594x + 4.5374$	0.8609
Funnel length (FL)	Dorsal mantle length (DML)	$y = 0.4905x + 3.2751$	0.7559
Arm length 2 (AL2)	Dorsal mantle length (DML)	$y = 1.8016x - 1.5714$	0.8773
Arm length 3 (AL3)	Dorsal mantle length (DML)	$y = 1.1550x + 5.5401$	0.8169
Arm length 4 (AL4)	Dorsal mantle length (DML)	$y = 0.8482x + 5.8121$	0.8292

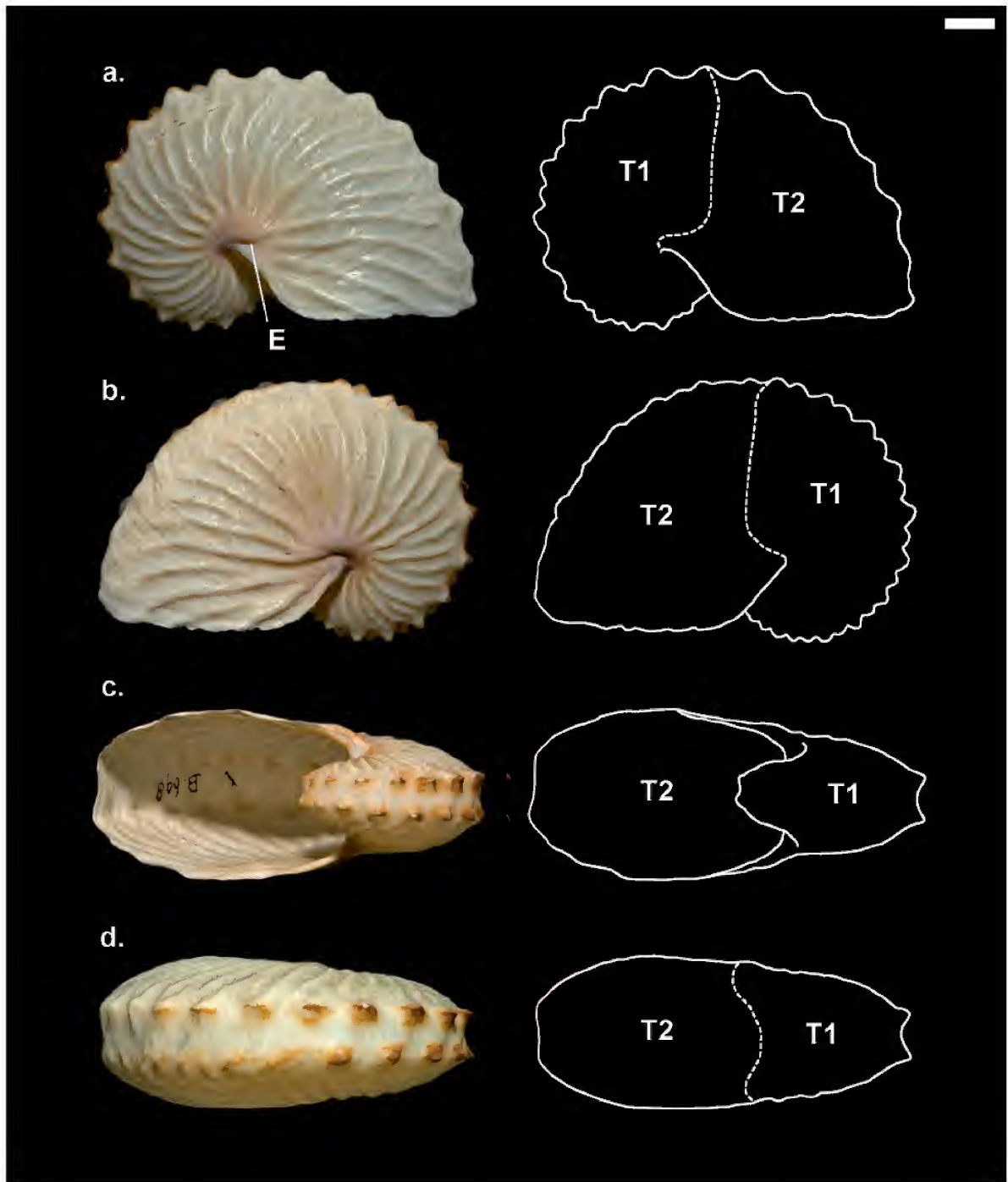


Figure 26. *Argonauta hians* shell from the British Museum: a–d, four perspectives of an *A. hians* shell from the British Museum (76.1 mm shell length [P], BMNH unreg., locality unknown, "B698, t.") which, while displaying an aperture shape and axial region consistent with the original description of *A. boettgeri* (fig. 22B, C), shows signs of possessing ears (E) at an earlier stage of growth; a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. A shift from Type 1 shell formation (T1) to Type 2 shell formation (T2) is expressed by ears subsumed and a reduction in keel tubercle size on the right side only. Scale bar = 1 cm.

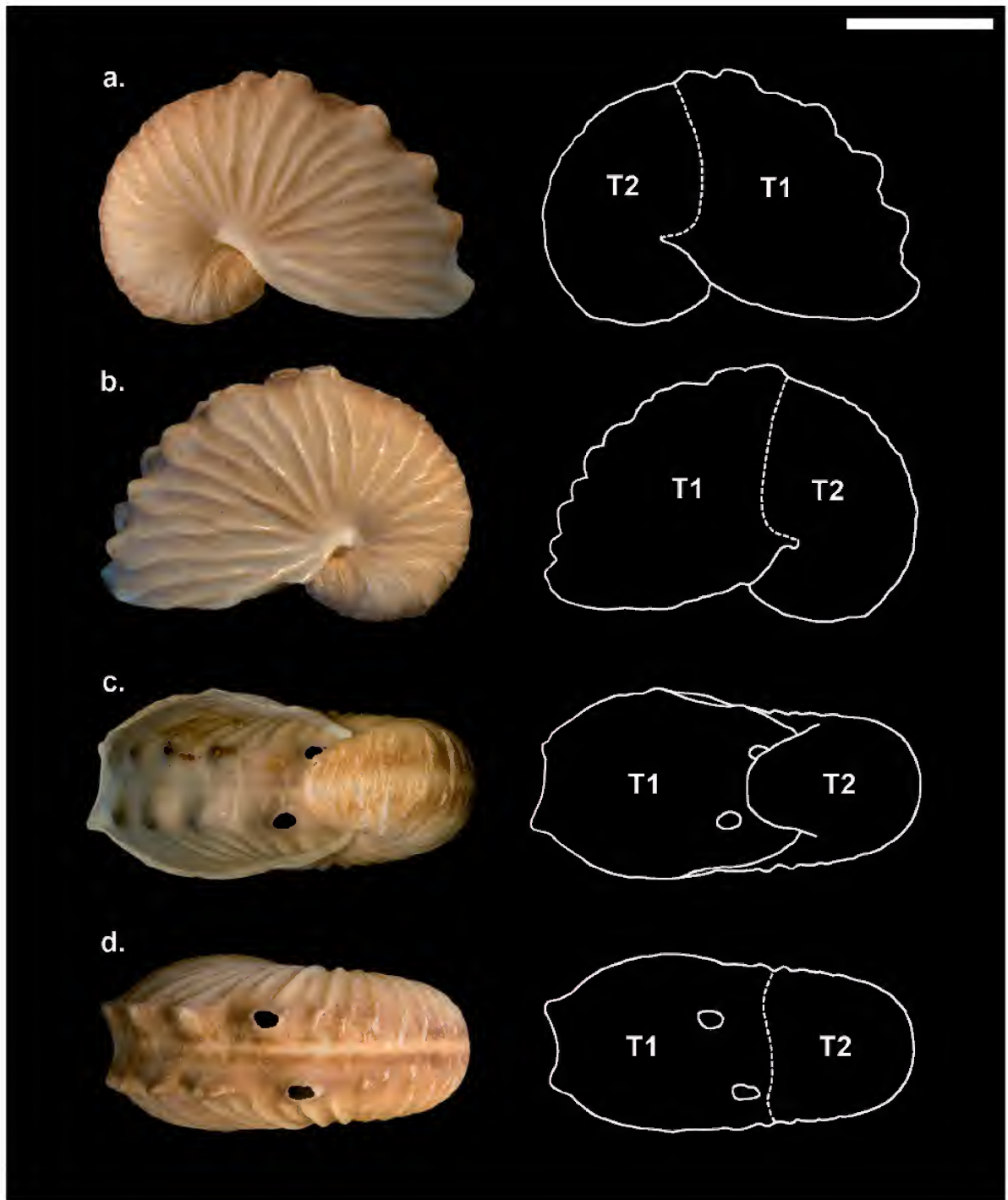


Figure 27. Shell consistent with description of *Argonauta boettgeri* from Museums Victoria: a–d, four perspectives of a shell consistent with *A. boettgeri* (treated here as a synonym of *A. hians* [Lightfoot], 1786) from Museums Victoria (25.0 mm shell length, NMV F164767) displaying an increase in keel tubercle size consistent with a shift from Type 2 shell formation (T2) to Type 1 shell formation (T1); a, left lateral view; b, right lateral view; c, anterior aperture view; d, posterior keel view. Scale bar = 1 cm.

Table 3. Linear regression equations for scatter plots of shell dimensions (y) against shell length (x) for 35 female *Argonauta hians* from Australian waters (WAM S31520/NMV 87104/QM Mo77789) including submature, mature and spawned individuals. Corresponding coefficients of determination (i.e. R^2 values) presented.

y	x	equation	R^2
Shell breadth (ShB)	Shell length (ShL)	$y = 0.7676x - 4.8377$	0.9015
Aperture length (ApL)	Shell length (ShL)	$y = 0.8013x - 2.6968$	0.9613
Aperture width (ApW)	Shell length (ShL)	$y = 0.3369x + 7.0488$	0.7752
Keel width (KW)	Shell length (ShL)	$y = 0.1701x + 2.7255$	0.8254
Ear width (EW)	Shell length (ShL)	$y = 0.2936x + 9.1011$	0.7391

Ontogenetic changes in animal morphology. Dimensions and characters of the female argonauts were plotted against DML to determine if the relative proportions of the female changes between submature, mature and spawned individuals. Scatterplots against DML were generated for MW, HW, FL and AL. The scatter plots indicate a linear relationship between animal dimensions, with linear regressions returning coefficient of determination values (i.e. R^2 values) between 0.76 and 0.88 (see Table 2). No discontinuities were observed between the three maturity stages.

Ontogenetic changes in shell morphometrics. Shell dimensions and characters were plotted against ShL to determine if relative shell proportions change between submature, mature and spawned females. Scatterplots against ShL were generated for ShB, ApL, ApW, KW and EW. The scatter plots indicate a linear relationship between shell dimensions and characters, with linear regressions returning coefficient of determination values (i.e. R^2 values) between 0.74 and 0.96 (see Table 3). No discontinuities were observed between the three maturity stages.

The scatter plots provided no evidence of a change in relative shell and animal proportions between submature, mature and spawned individuals. If the examined characters underwent dramatic transformation with changes in state of maturity, it was expected that discontinuities would be observed in the plotted data. It is apparent that the visual change in shell form observed across this lot was not reflected in the relative measurements of the individuals measured.

***Argonauta nodosus* [Lightfoot], 1786; the *A. nodosus/tuberculatus* complex**

The original description of *A. nodosus* [Lightfoot], 1786, refers to a single image in Rumphius (1705): plate 18, figure 1 (fig. 28a), designated as a lectotype by Moolenbeek (2008) in the absence of type material. Shells of *A. nodosus* can be recognised by the presence of lateral ribs composed of separate tubercles.

Two types of *A. nodosus* shells exist in collections: a finer shell with more ribs and small rib tuberculations (fig. 29a), and a coarser shell with fewer ribs and larger rib tuberculations (fig. 29b).

This variation has previously been used as justification for splitting *A. nodosus* into two species. Kirk (1885), in recognising the two forms, generated a new species name for the fine tuberculated and earless form (*A. gracilis*) to separate it from the coarse tuberculated and eared form (known to Kirk, 1885, as *A.*

tuberculata Shaw). Robson (1932) recognised the two shell types as varieties, not separate species, stating: “Though the shell of this species is clearly distinguished from its fellows by the rough tuberculations, there are evidently two well marked varieties – one with very large carinal knobs and coarse sculpture, the other with low knobs and fine sculpture” (p. 200). Dell (1952) called this the “*nodosa-tuberculata* complex”² and described it as follows: “Group 1. The shell is eared laterally and the tuberculations on the ribs are comparatively large – this is what has been called *nodosa*. Group 2. The edge of the lip comes off the previous whorl in an even curve without trace of an ‘ear’. The tuberculations are much finer and more numerous than in Group 1 – *tuberculata*” (p. 54). Dell (1952) considered both forms to belong to a single species.

While both shell varieties are common, individual shells displaying an obvious shift between fine and coarse shell formation are extremely rare. A single shell from Moreton Bay, Queensland (109.1 mm ShL, QM Mo14232) displays a transition from fine shell formation to coarse shell formation at a point of previous damage (fig. 30). While the later component of the shell possesses ears, it is not clear whether the earlier component was eared or earless. No obvious changes were noted in shell thickness, curvature of the keel or relative heights of sequential keel tubercles.

Examination of a large number of *A. nodosus* shells found no examples displaying a marked change in keel tubercle height or ears that had been formed or subsumed. While eared and earless forms exist, transition between the two types appeared more gradual than the sudden transformation documented in smaller species. A shell in the British Museum (109.0 mm ShL [P], BMNH unreg., locality unknown, “B395, e.”) displays an ear on only one side, clearly demonstrating the plasticity of this character in this species (fig. 31).

² Following Finn (2013) it is necessary to correct the original spelling of *A. nodosa* to *A. nodosus*. In accordance with the *International Code of Zoological Nomenclature*, Article 34.2 “the ending of a Latin or latinized adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined [Art. 31.2]; if the gender ending is incorrect it must be changed accordingly (the author and date of the name remain unchanged)” (I.C.Z.N., 1999). As *Argonauta* is masculine “from the final noun *nauta* (a sailor)” (I.C.Z.N., 1999, p. 34) the species-group name must be changed from the feminine *nodosa* (-a feminine) to the masculine *nodosus* (-us masculine).

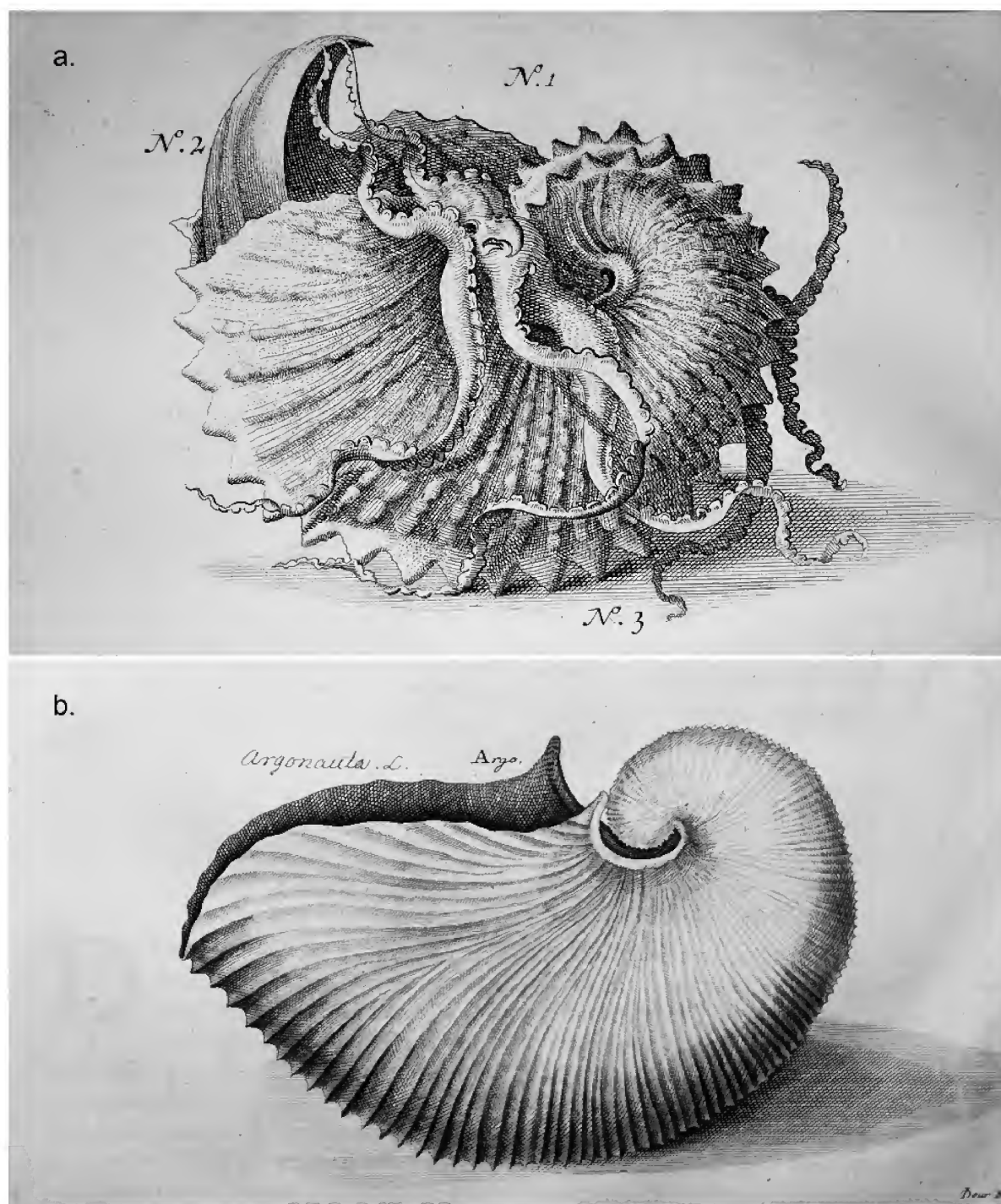


Figure 28. Reproduced illustrations referenced in the descriptions of *Argonauta nodosus* [Lightfoot], 1786 and *A. argo* Linnaeus, 1758: a, illustration of *A. nodosus* [Lightfoot], 1786, designated as a lectotype by Moolenbeek (2008), Rumphius 1705, pl. 18, fig. 1; b, illustration of *A. argo* Linnaeus, 1758, considered a paralectotype following the designation of a lectotype by Moolenbeek (2008), Rumphius 1705, pl. 18, fig. A.

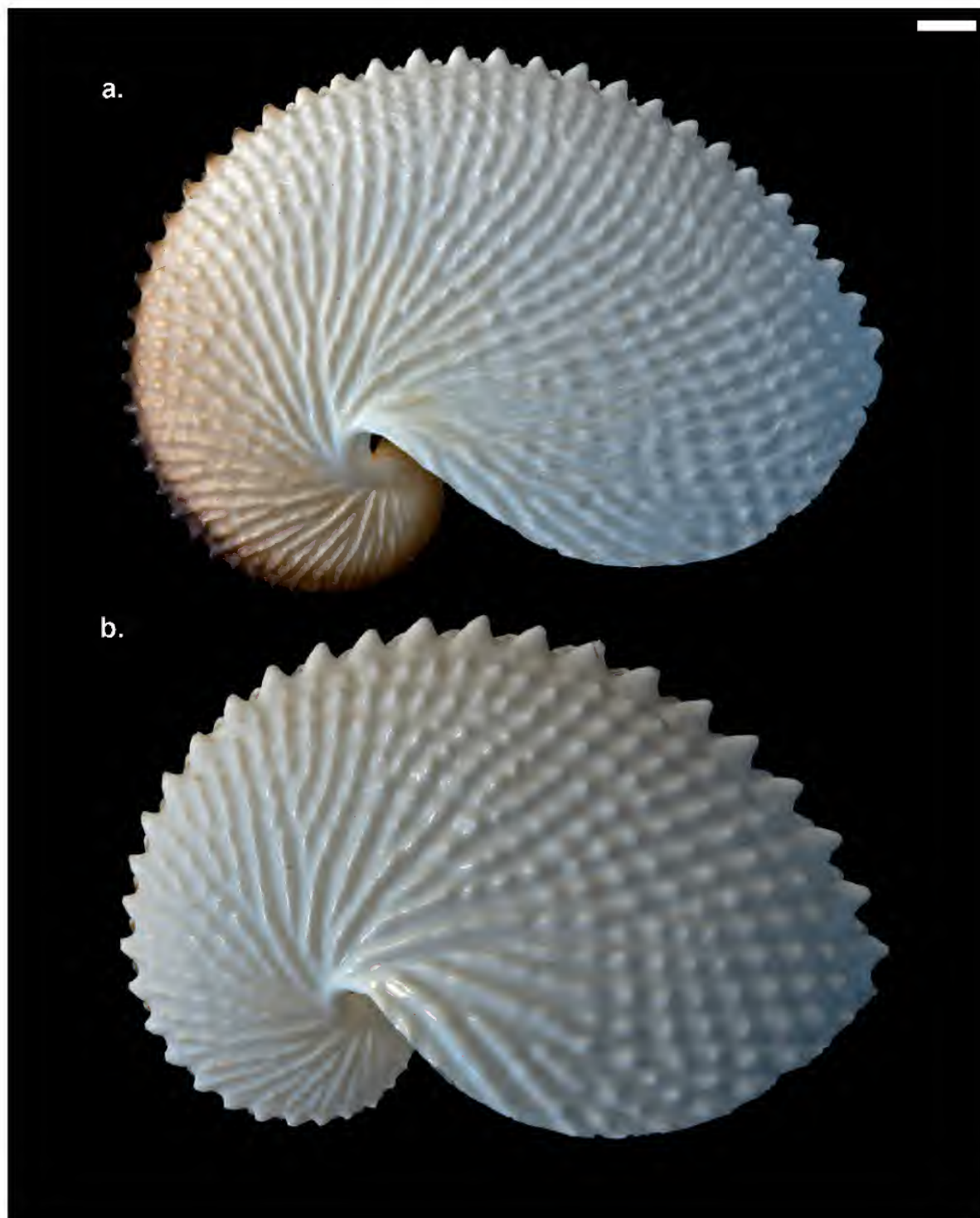


Figure 29. Coarse and fine *Argonauta nodosus* shells: a, fine *A. nodosus* shell from Mayor Is., Bay of Plenty, New Zealand (127.2 mm shell length, NMV F164784); b, Coarse *A. nodosus* shell from the Indo Pacific (127.3 mm shell length, NMV F164774). Scale bar = 1 cm.

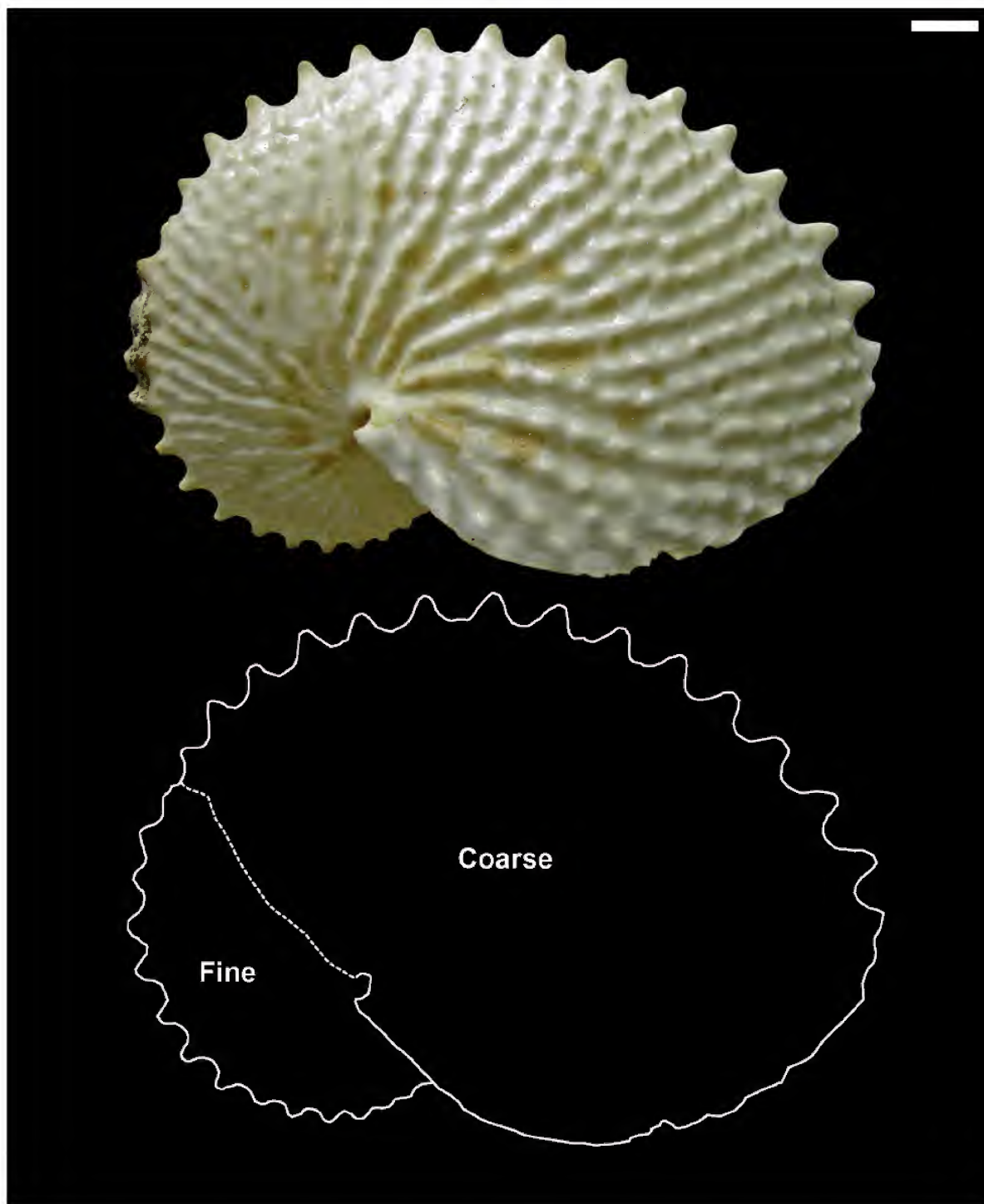


Figure 30. Repaired *Argonauta nodosus* shell from Moreton Bay, Queensland. Left lateral view of repaired *A. nodosus* shell from Moreton Bay, Queensland (109.1 mm shell length, QM Mo14232) showing a transition from fine shell formation (Fine) to coarse shell formation (Coarse) at point of previous damage. Scale bar = 1 cm.

Argonauta argo Linnaeus, 1758

An image referenced in the original description of *A. argo* Linnaeus, 1758, is considered a paralectotype, with designation of a lectotype by Moolenbeek (2008); Rumphius, (1705) plate 18 figure A (fig. 28b). Shells of *A. argo* can be recognised by an extremely narrow keel of consistent width. The keel tubercles are paired and the lateral ribs are continuous (i.e. they are not broken into separate tubercles).

Shells of *A. argo* are extremely consistent in dimensions and sculpturing. The area that has caused the most confusion for naturalists defining the species has been the aperture edge. *A. argo* can display huge variation in the shape of the aperture edge near the axis. Note the variation in the aperture edge of the two shells presented in fig. 32. Unlike ear formation, this variation occurs on the edge of the lateral wall parallel with the longitudinal axis of the shell; it is not a lateral extension. The expression of the lateral ribs can vary slightly from fine to coarse, suggesting the presence of two varieties (fig. 32). Transition between fine and coarse shell formation on a single shell is extremely rare. An illustrated shell from Monterey, California (81.9 mm ShL, USNM 61374) displays a shift from finer to coarser shell formation at the point of earlier damage (fig. 33). Small *A. argo* shells can also display laterally protruding ears. A shell from Venezuela (51.4 mm ShL, USNM 122208) highlights the plasticity of this character, displaying an ear on only the right side (fig. 34). The varied size and shape of the keel tubercles on the opposing sides of this shell demonstrate the range of variability of these structures in this species.

Discussion

Among molluscs, the shells of small argonaut species (in particular, *A. nouryi*) display an unprecedented level of variability. The extreme forms are so different that it initially seems incomprehensible that they could be produced by the same argonaut species. Given this apparent disparity, it is necessary to emphasise that argonaut shells are fundamentally different in nature from the true molluscan shells of non-cephalopod molluscs; they are produced by different structures, for different reasons and have a different construction.

Shell material laid down by females of small argonaut species (*A. nouryi* and *A. hians*) can take one of two distinct morphologies. Firstly, the shell can be heavy and thick walled with prominent sculpture (Type 1 shell formation). The large corrugations of the lateral walls are displayed as distinct robust lateral ribs. The thickened keel is defined by two rows of large and distinct keel tubercles. The axis of the shell projects laterally to form large ears, providing support to the lateral walls. In the second form, the shell can be lightweight and thin walled, with greatly reduced sculpture (Type 2 shell formation). The corrugations of the lateral walls are downgraded to fine lateral ribs. The convex keel is undefined, with the keel tubercles diminished to slight projections of the lateral rib extremities. The axis of the shell is rolled ventrally to join the aperture edge without lateral projection (i.e. earless).

The shell morphology expressed by a growing female argonaut does not follow a predetermined order. Shells of female *A. nouryi* demonstrate that females can switch between

the two shell formation types at least three times during production of a single shell. The initial shell formation type is variable (it can be Type 1 or Type 2), as is the portion of shell laid down before switching to another shell formation type.

It is largely impossible to determine the conditions an argonaut was exposed to at the time that it switched shell formation types. The exception is the response to shell breakage. Individual shells retain evidence of earlier trauma in the form of repairs and irregularities in shell form. *A. nouryi* shells almost invariably display a shift to Type 2 shell formation following major damage. At the time of shell breakage, an argonaut would be exposed and vulnerable. As has been observed for *A. argo*, shell integrity is critical in allowing the argonaut to attain neutral buoyancy, free itself from the sea surface and undertake rapid horizontal locomotion (Finn and Norman, 2010). In the absence of shell-aided buoyancy, the female must remain in the water column by siphon-jetting alone. As such, it would be imperative for a female argonaut to rebuild her shell as quickly as possible following any damage. It is assumed that the shift to thinner walled Type 2 shell formation allows the female to rebuild her shell more rapidly, spreading the available building material (calcium carbonate) over a greater area.

The different morphologies expressed in an individual *A. nouryi* shell are therefore considered to represent periods of varied rate of shell formation. Components of a shell laid down over longer periods are believed to exhibit thicker walls and more prominent sculpture (Type 1), while rapidly produced sections display thinner walls and reduced sculpture (Type 2). The rate at which the female lays down the shell is believed to determine the gross morphology of the shell. Based on this presumption, two hypotheses are raised to explain the variable shell production rate (expressed as the variable shell formation type) evident in undamaged, unrepaired shells:

- **Hypothesis 1: Rate of shell production correlates directly with animal growth.** Three factors are believed to influence octopus growth rate: temperature, nutrition, and maturation or reproduction (see Semmens et al., 2004 for a review). While very little is known about the lives of argonauts, they are known to occur in the open ocean spanning huge geographical distributions. This wide-ranging pelagic existence has the potential to expose them to a mosaic of food availability and water temperatures. Encountering a large school of prey or pocket of warmer water may result in a period of increased growth. Additionally, reproductive investment (i.e. egg production) may slow body growth. This hypothesis suggests that these periods of varied morphological growth of the animal are reflected in the gross morphology of the shell.
- **Hypothesis 2: Rate of shell production influenced by external factors.** The shells of female argonauts, in addition to providing protection and buoyancy, primarily function as a case for external brooding of the female's eggs. Strings of eggs are suspended from the inner core of the shell. This strategy requires that the internal volume of the shell accommodate both the female argonaut and her eggs. This hypothesis proposes that the space constraints associated with commencement of egg

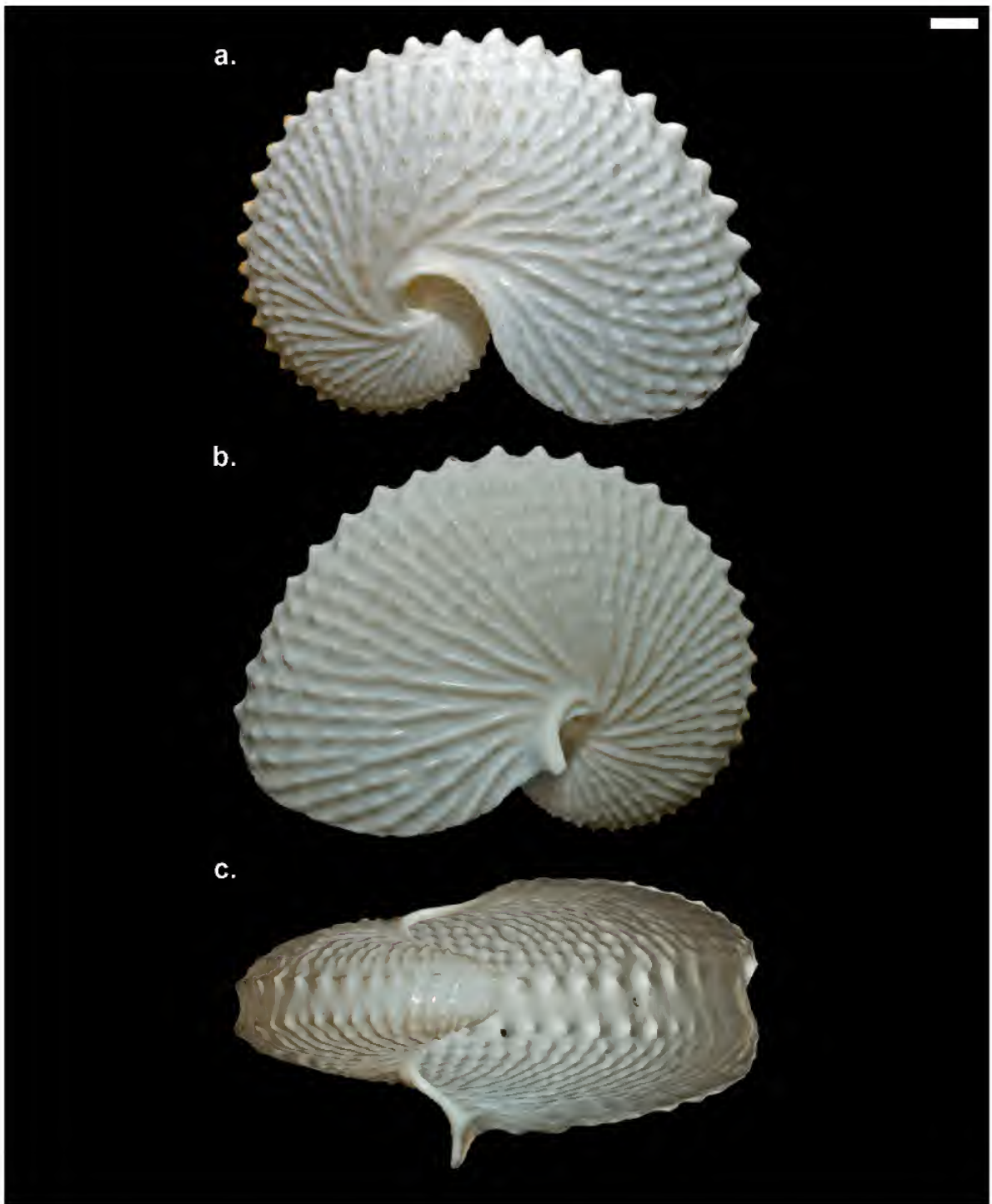


Figure 31. Single eared *Argonauta nodosus* shell from the British Museum: a–c, three perspectives of a single eared *A. nodosus* shell from the British Museum (109.0 mm shell length [PJ, BMNH unreg., locality unknown, “B395, e.”]); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

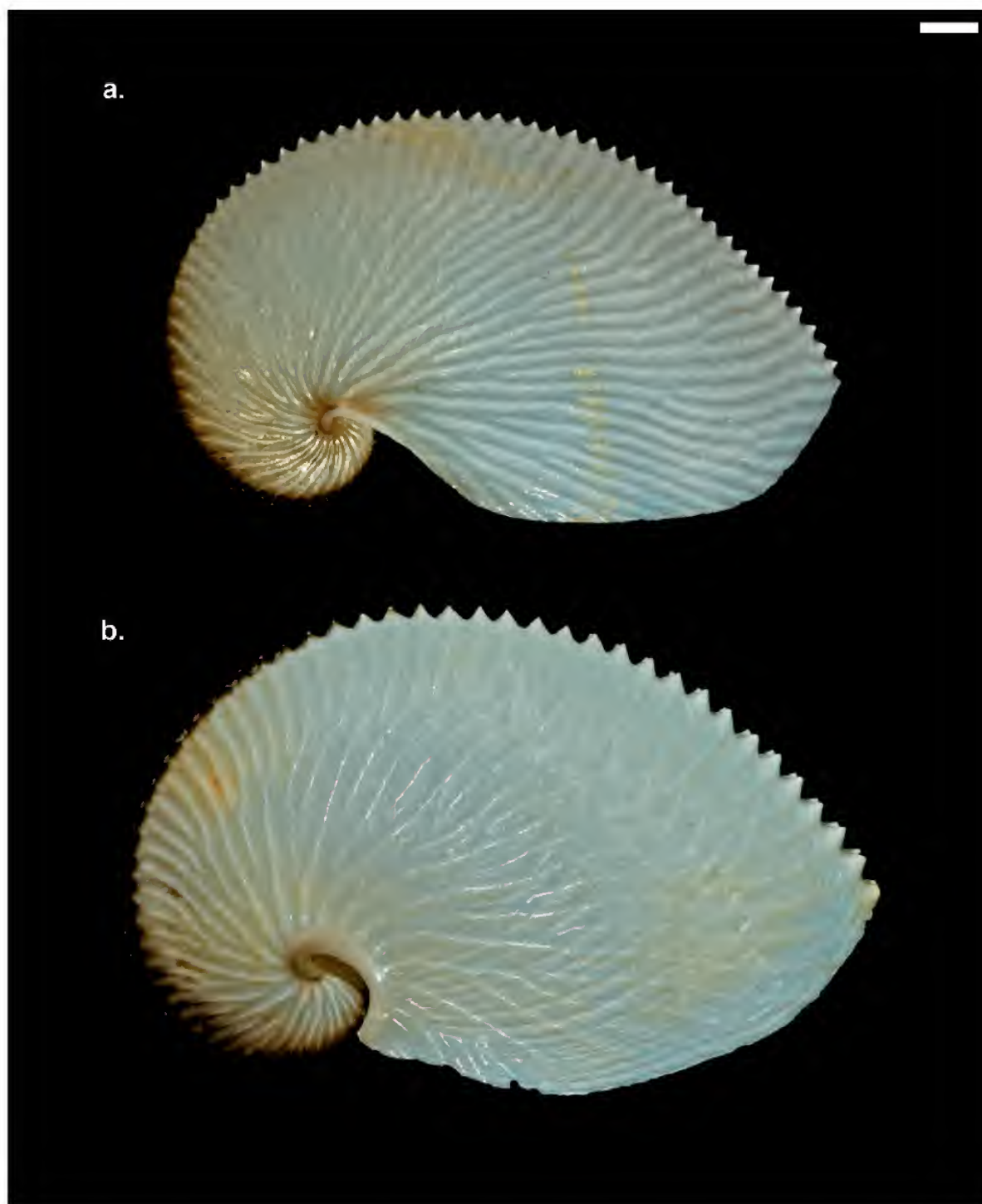


Figure 32. Coarse and fine *Argonauta argo* shells: a–b, shells of *A. argo* displaying different degree of sculpturing and variation in the aperture edge; a, fine *A. argo* shell from off San Clement Island, California (113.3 mm shell length [P], USNM 316580); b, coarse *A. argo* shell from Baja California (128.1 mm shell length [P], ANSP 404279). Scale bar = 1 cm.

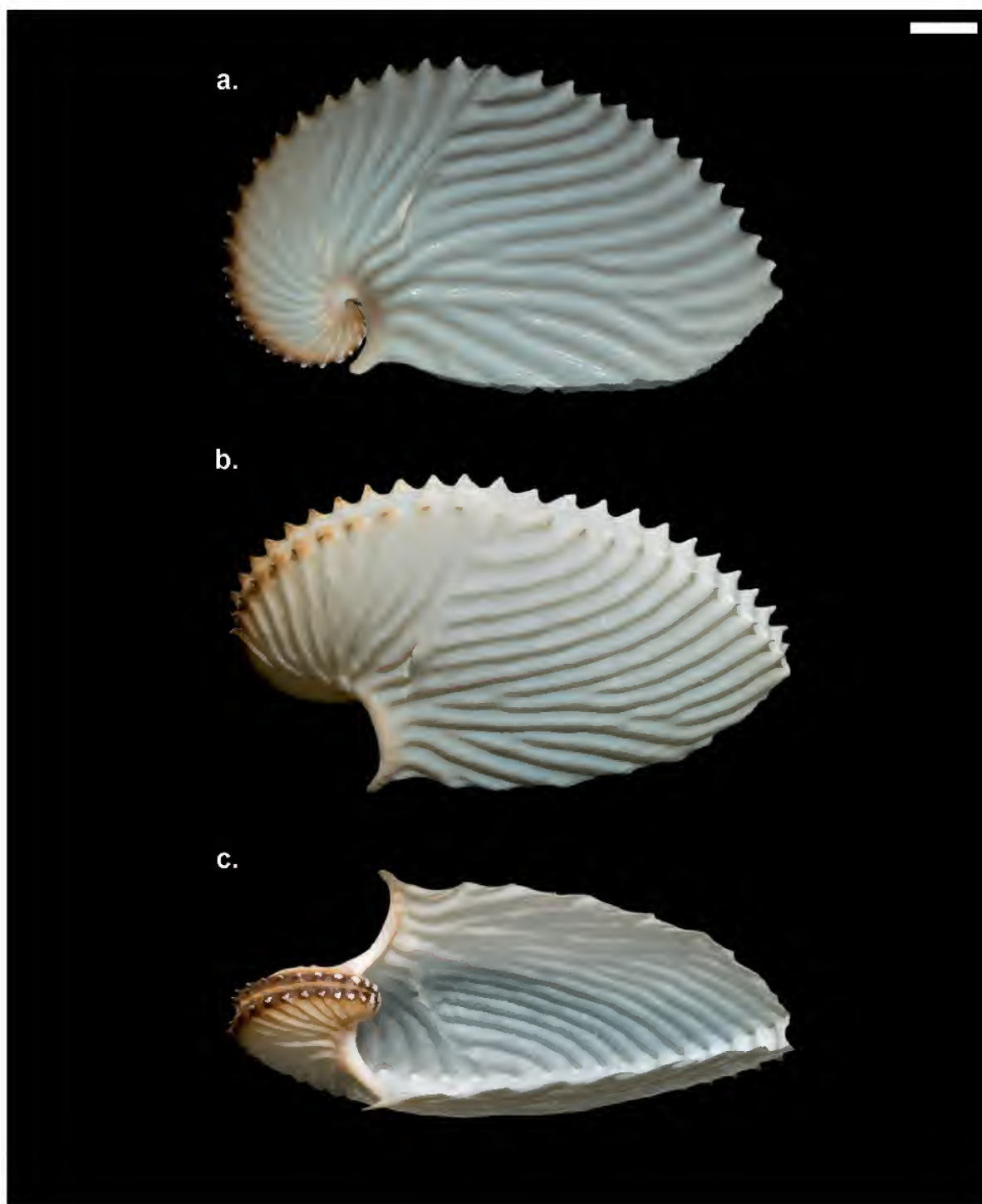


Figure 33. Repaired *Argonauta argo* shell from Monterey, California. Repaired *A. argo* shell from Monterey, California (81.9 mm shell length, USNM 61374): a, left lateral view; b, oblique left lateral view; c, oblique anterior aperture view. Note change in direction of lateral ribs along repair line. Scale bar = 1 cm.

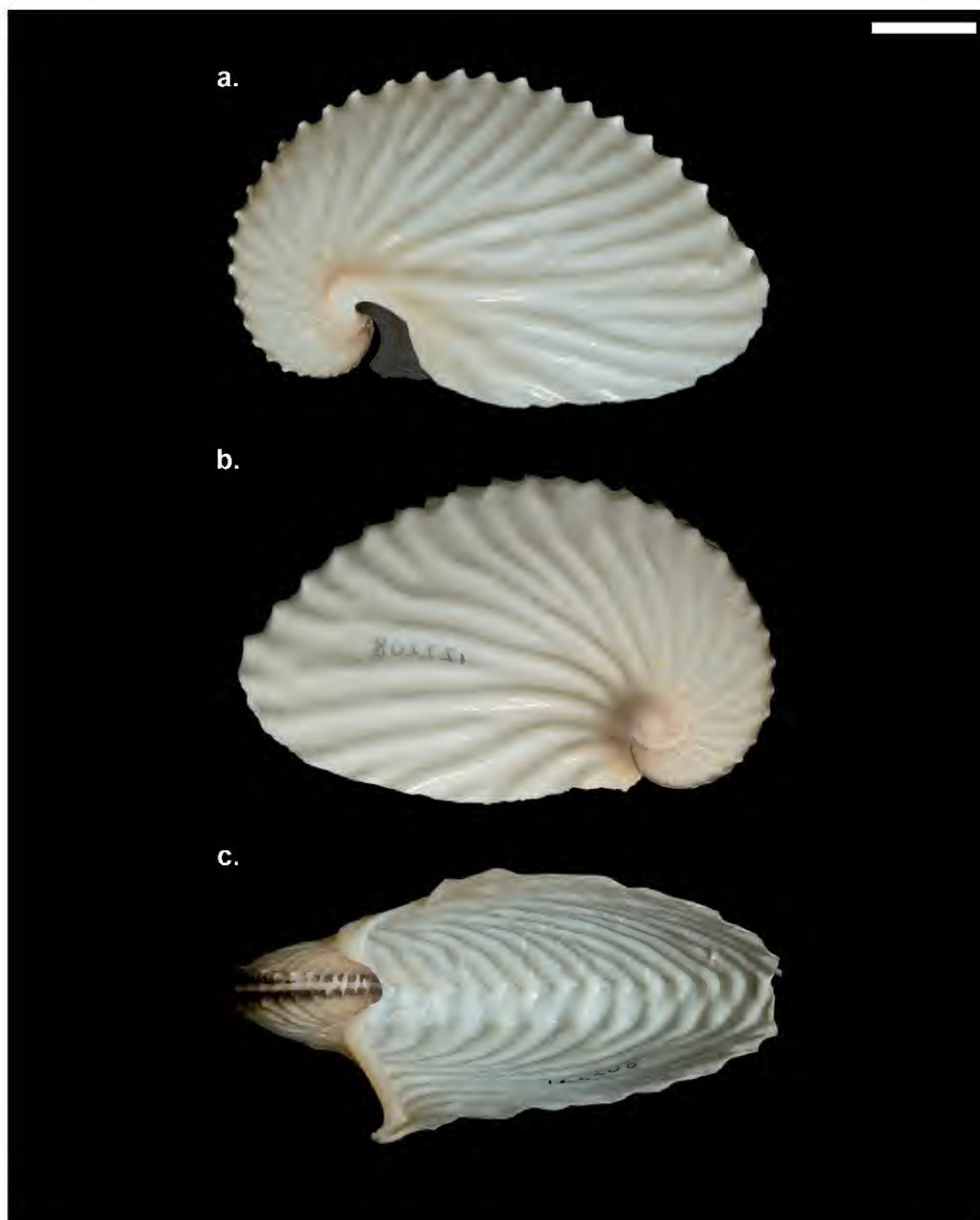


Figure 34. Single eared *Argonauta argo* shell from Venezuela, South America: a–c, three perspectives of a single eared *A. argo* shell from Venezuela (51.4 mm shell length, USNM 122208); a, left lateral view; b, right lateral view; c, anterior aperture view. Scale bar = 1 cm.

spawning triggers an increase in shell production rate. The gross morphology of the shell therefore displays intermittent periods of volume constraints as a result of intermittent spawning or brooding events.

To gain insights into the relationships between features of the argonaut shell and its female occupant, focus was directed at *A. hians*. The large single lot of female *A. hians* (with accompanying shells) from Western Australia includes three classes: submature, mature (unspawned) and spawned individuals. Examination of the lot revealed that all spawned individuals (i.e. all individuals with eggs deposited within their shells) displayed a shift from Type 1 to Type 2 shell formation. No converse arrangements were observed. Based on this qualitative observation, this large sample appeared to support Hypothesis 2; the presence of spawned eggs within the shell causing a space constraint and thus triggering a shift to more expansive thin-walled shell production. Hypothesis 1 would predict slower body growth of the argonaut associated with increased reproductive investment in egg production. This would predict slower shell production and hence a shift to Type 1 formation. This was not observed. Quantitative analysis of argonauts in this lot did not provide further insight. A full range of characters of both the animals and shells were measured. Features of the shell, the female and the shell relative to the female were compared, plotted and analysed with linear regression. In all instances, scatter plots indicated linear relationships between animal and shell dimensions, with linear regressions returning high coefficients of determination values (i.e. R^2 values) with no discontinuities observed between submature, mature and spawned individuals.

Examination of shells of larger species (*A. nodosus* and *A. argo*) revealed that they are not subject to the extreme variability in shell form identified in the smaller argonaut species. While both large species display two distinct morphologies (coarse and fine forms), the two shell types are never expressed as alternations on individual shells. Rare examples of extremely damaged shells can display a shift from fine to coarse morphology, but a reversion (i.e. from coarse to fine) was never observed. Because the two shell types do not vary in shell wall thickness or amount of material used, the variation between the two shell types appears fundamentally different from that observed in smaller species. One possible explanation is that the coarser shells of larger species represent reformed shells produced by large individuals (i.e. new shells constructed to replace lost or damaged shells), while the finer shells represent the original shells that are produced as the animals grow.

In the absence of captive rearing studies and sequential collections of the same argonaut species from the same location, it is not possible to conclusively support either hypothesis. Based on limited observational evidence, it is the author's opinion that the variation observed in the shells of small argonaut species is the result of space constraints (i.e. Hypothesis 2) and independent of argonaut growth. The prime circumstantial evidence comes firstly from gross differences in shell occupation between large and small species, and secondly from the dramatic transformation or reversion boundaries on the shells of small species.

Gross differences in shell occupation. At commencement of egg laying, the shells of females of small argonaut species possess an extremely small amount of available space for egg storage. Fig. 35a shows a preserved female *A. nouryi* that had already commenced egg laying with a DML of 15.2 mm (SBMNH 64369). As can be seen from the image, the space at the top of the shell where the eggs are to be stored is extremely small. The shell has barely formed through 90 degrees. Storage of egg-strings within this shell will have a significant impact on the space available for this small female within the shell. Fig. 35b shows a female *A. hians* with a DML of 28.7 mm (QM Mo77789). Yellow eggs are clearly visible and occupy almost half of the shell volume. While the shell has developed through almost a complete rotation, the volume occupied by the eggs significantly displaces the female. With the posterior tip of the mantle firmly against the egg mass, the female is still only partially within her shell. Note the distance of the eye from the edge of the shell aperture. In the absence of eggs, female argonauts typically retract well into their shells with their eyes at the boundary of the lateral walls. Fig. 36a presents a photograph of a live female *A. hians* photographed in an aquarium (after Sukhsangchan and Nabhitabhata, 2007). With a large volume of eggs in the initial whorl of the shell, the female can only partially retract within. The aperture edge of the shell sits posteriorly to the mantle edge and a considerable distance from the female's eye.

Displacement of the female from the shell would provide a strong stimulus for rapid shell deposition, resulting in the extended flange-like form of Type 2 shells. Subsequent interruptions to egg production (or hatching) could explain a return to full occupancy of the shell and Type 1 shell formation, as demonstrated in *A. nouryi*.

The apparent space constraint observed in smaller species is not evident in larger species. Females of *A. nodosus*, observed live, appear uninfluenced by large volumes of eggs held within their shells. Fig. 36b presents a photograph of a live female *A. nodosus*. This female is positioned well within her shell; note the proximity of the female's eye to the edge of the shell aperture. Although not apparent from this photograph, the female is carrying a huge volume of eggs. Fig. 36c presents the egg strings revealed on removal of the female from her shell.

It is possible that the increased size of the shell of larger species at the commencement of egg laying enables egg and female accommodation. The shells of female *A. nodosus* are considerably more developed than those of smaller species when spawning commences; five females with ShL ranging from 54.6 to 62.1 mm (and DML ranging from 31.1 to 38.5 mm) were found to still be immature (see Finn, 2013, for details).

Immediacy of transformations and reversions. Additional qualitative support comes from the abrupt nature of shell transformations and reversions. Shells of female *A. nouryi* display obvious precise boundaries between shell formation types. It is the author's opinion that the distinct boundaries between shell formation types indicates that the causal stimulus acts instantaneously on the female. It is felt that spawning of eggs would have an immediate effect, requiring the female to abruptly change the way the shell material is laid

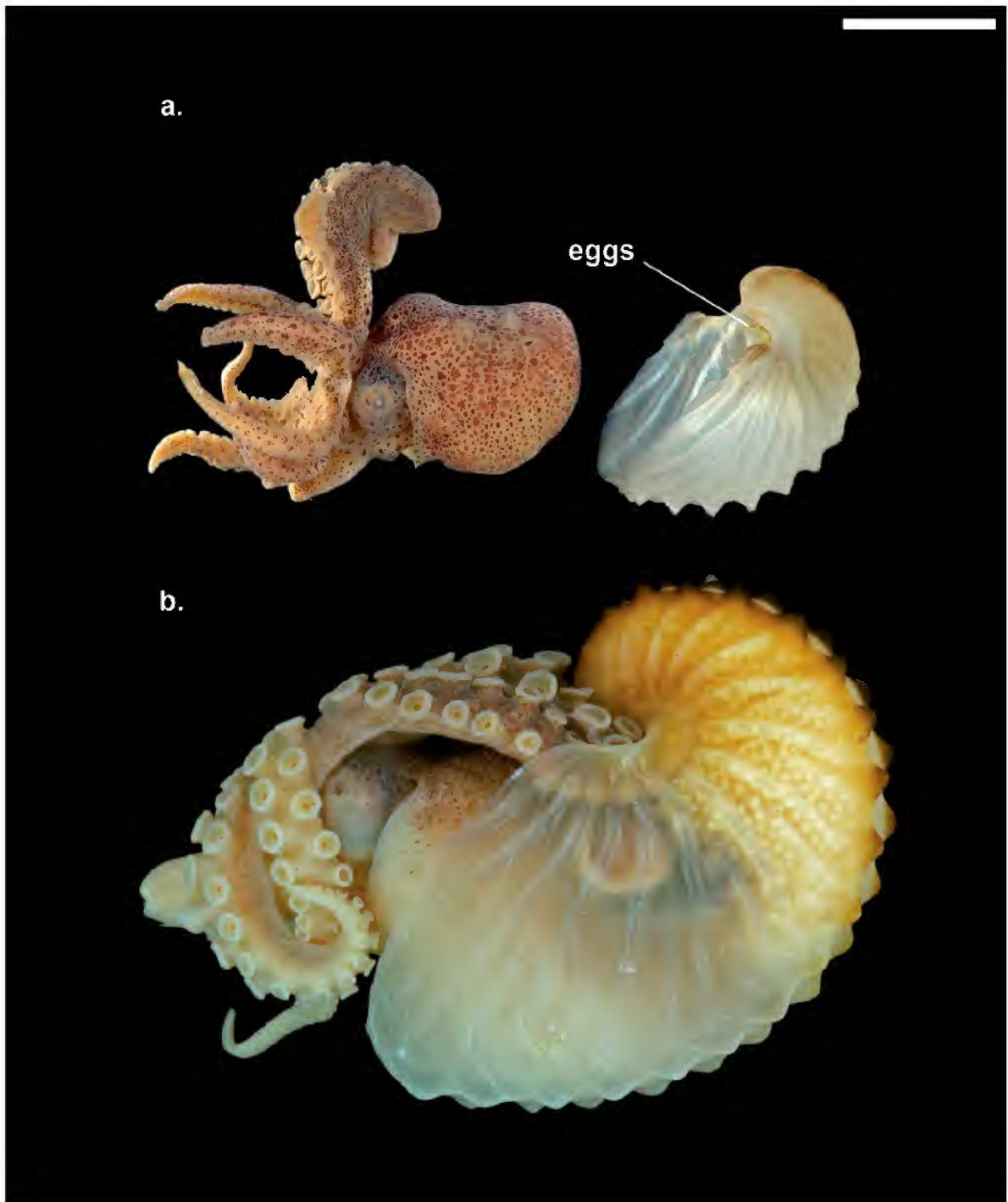


Figure 35. Preserved female *Argonauta nouryi* and *A. hians* with spawned eggs: a, preserved female *A. nouryi* from the Pacific Ocean (15.2 mm dorsal mantle length, 18.4 mm shell length, SBMNH 64369) with spawned eggs attached to the axis of the shell; b, preserved female *A. hians* from the North West Shelf, Western Australia (28.7 mm dorsal mantle length, 38.9 mm shell length, QM Mo77789) with yellow eggs visible in dorsal component of shell. Scale bar = 1 cm.



Figure 36. Images of live female argonauts, *Argonauta hians* and *A. nodosus*, demonstrating the effect of spawned eggs on the position of the females relative to their shells: a, live female *A. hians* from Andaman Sea, Thailand, photographed in an aquarium (photo: J. Nabhitabhata, after Sukhsangchan and Nabhitabhata 2007); b–c, *A. nodosus* Phillip Bay, Victoria, Australia (photos: R. Kuiter); b, live female argonaut photographed in the wild; c, eggs of same specimen, shown with argonaut removed from shell.

down to accommodate the increased volume. If a change in the growth rate was responsible for the transformation between shell formation types, it is believed that the transition would be more gradual and the boundaries in the shell less pronounced.

Argonaut nomenclature and the fossil record.

Misinterpretation of intra-specific shell variation has hindered the resolution of extant argonaut systematics. Historic generation of species names based on individual malformed shells, and shells of different formation types, has created confusion and complication. Fortunately, this practice has largely ceased. The last major erection of new species names occurred in 1914 when Monterosato proposed three new species names and one variety based on four shells of *A. argo* (Monterosato 1914). Interpretation of the fossil record, however, appears to be mirroring the historic approach applied to extant argonauts. Variation in shell characters is continuing to be used to designate new fossil argonaut species (Stadum and Saul, 2000), and many have been erected based on single fossilised shells (e.g. Martill and Barker, 2006). Saul and Stadum (2005) reviewed the current situation stating: “ten fossil argonaut species have been placed into four genera based on the absence or presence of keels and the degree of sculpture” (p. 520). If the situation is at all similar to that of extant argonauts, great caution should be undertaken when erecting fossil argonaut species based solely on shell characters.

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The *Eiconaxius cristagalli* species complex (Decapoda, Axiidea, Axiidae)

(<http://zoobank.org/urn:lsid:zoobank.org:pub:FFB0A3E1-53D8-416B-8E22-49ED61081AE5>)

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Abstract

Poore, G.C.B., and Dworschak, P.C. (2018). The *Eiconaxius cristagalli* species complex (Decapoda, Axiidea, Axiidae). *Memoirs of Museum Victoria* 77: 105–120.

Four species of *Eiconaxius* are known to possess a denticulate median rostral carina: *E. antillensis* Bouvier, 1905, *E. asper* Rathbun, 1906, *E. cristagalli* Faxon, 1893, and *E. indicus* (De Man, 1907). They are reviewed and two similar new species are described: *E. dongshaensis* sp. nov., and *E. gololobovi* sp. nov. A key to distinguish them is presented.

Keywords

Crustacea, Decapoda, Axiidae, *Eiconaxius*, new species

Introduction

The axiid genus *Eiconaxius* Bate, 1888 comprises more than 30 species confined to deep water that are, as far as is known, associates of sponges (Komai and Tsuchida, 2012). A few species differ from all others in having a prominent median denticulate crest on the rostrum reaching back to the gastric region where it bifurcates. In all other species this ridge is low and smooth, or at best only slightly serrate. Faxon (1893), who used the species epithet *cristagalli* for the first species in this group alluded to a cock's comb and described the ridge as bearing 'prominent teeth'. Three more similar species were described shortly thereafter (Bouvier, 1905; Rathbun, 1906; De Man, 1907). These four are rediagnosed and two new similar species are described from the Indo-West Pacific.

Methods

The material comes from: the Muséum nationale d'Histoire naturelle, Paris (MNHN) expeditions to Guadeloupe, (KARUBENTHOS 2016) and to the Mayotte-Glorieuses region, 2017 (BIOMAGLO); four expeditions by MNHN-ORSTOM (Office de la recherche scientifique et technique outre-mer, now IRD Institut de recherche pour le développement) (see <http://expeditions.mnhn.fr/> and Richer de Forges et al., 2013); collections made by the National Taiwan Ocean University, Keelung (NTOU) in the South China Sea; and the IUCN Seamounts expedition to the southwestern Indian Ocean, 2011 (Rogers and Taylor, 2012), material now lodged in Naturhistorisches Museum, Vienna (NHMW).

Type material consulted and types of new species are lodged in the Naturalis Biodiversity Center, Leiden (ZMA), Museums Victoria, Melbourne (NMV) and the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ). Other specimens were viewed in the National Museum of Natural History, Washington (USNM).

Size is expressed as carapace length, including rostrum, in mm. Relative lengths of fixed fingers of chelipeds are expressed as $(a-b)/b$ where a is the length of the lower margin of the propodus, including the fixed finger, and b is the length of the upper margin.

As part of this study and continuing discovery of new species in the Indo-West Pacific diagnoses have been prepared for all species of *Eiconaxius* and coded into a DELTA database (Dallwitz, 2010). This database was used to generate the diagnoses presented here; character states in italics diagnose each species in at least two respects from every other species. The poorly known *Eiconaxius asper* Rathbun, 1906 is diagnosed on the basis of its description but not included in the key.

Family Axiidae Huxley, 1879

Eiconaxius Bate, 1888

Eiconaxius Bate, 1888: 40. – Poore, 2017: 365–366.

Remarks. Poore (2017) provided a new diagnosis and discussed the synonymy of the genus. The following key deals only with species having a prominent median denticulate crest on the rostrum reaching back to the gastric region.

Key to species of *Eiconaxius cristagalli* species complex

1. East Pacific or Caribbean species 2
- Indo-West Pacific species 3
2. Rostrum triangular, tapering, median carina with 6 or 7 teeth; lateral carina without clear hiatus between posterior extension of rostral margin and posterior section; East Pacific *E. cristagalli* Faxon, 1893
- Rostrum tapering more steeply anteriorly, median carina with >10 teeth (Figs 1b, 2b); lateral carina with a clear hiatus between posterior extension of rostral margin and posterior section (Figs 1b, 2b); Caribbean *E. antillensis* Bouvier, 1905
3. Major cheliped palms fixed finger cutting edge crenellate (Fig. 5f, g); rostrum parallel-sided basally, tapering steeply anteriorly; lateral carina continuous from lateral margins of rostrum, with short overlap posteriorly (Fig. 5c); Western Indian Ocean *E. gololobovi* sp. nov.
- Major cheliped palms fixed finger cutting edge with simple blade (Figs 3e, f, 9g, h); rostrum tapering evenly from base to acute apex; lateral carina usually with considerable hiatus between lateral margins of rostrum and posterior section, or absent (Figs 3c, 9c) 4
4. Rostrum with ventral tooth (Fig. 3b); major cheliped, distolateral margin of propodus with 2 teeth at base of dactylus, lobe and narrow keyhole-shaped notch in gape (Fig. 3e); East China Sea *E. dongshaensis* sp. nov.
- Rostrum without ventral tooth (Fig. 9b); major cheliped, distolateral margin of propodus straight at base of dactylus, circular notch in gape (Fig. 9g); SW Pacific *E. indicus* (De Man, 1907)

***Eiconaxius antillensis* Bouvier, 1905**

Figures 1, 2

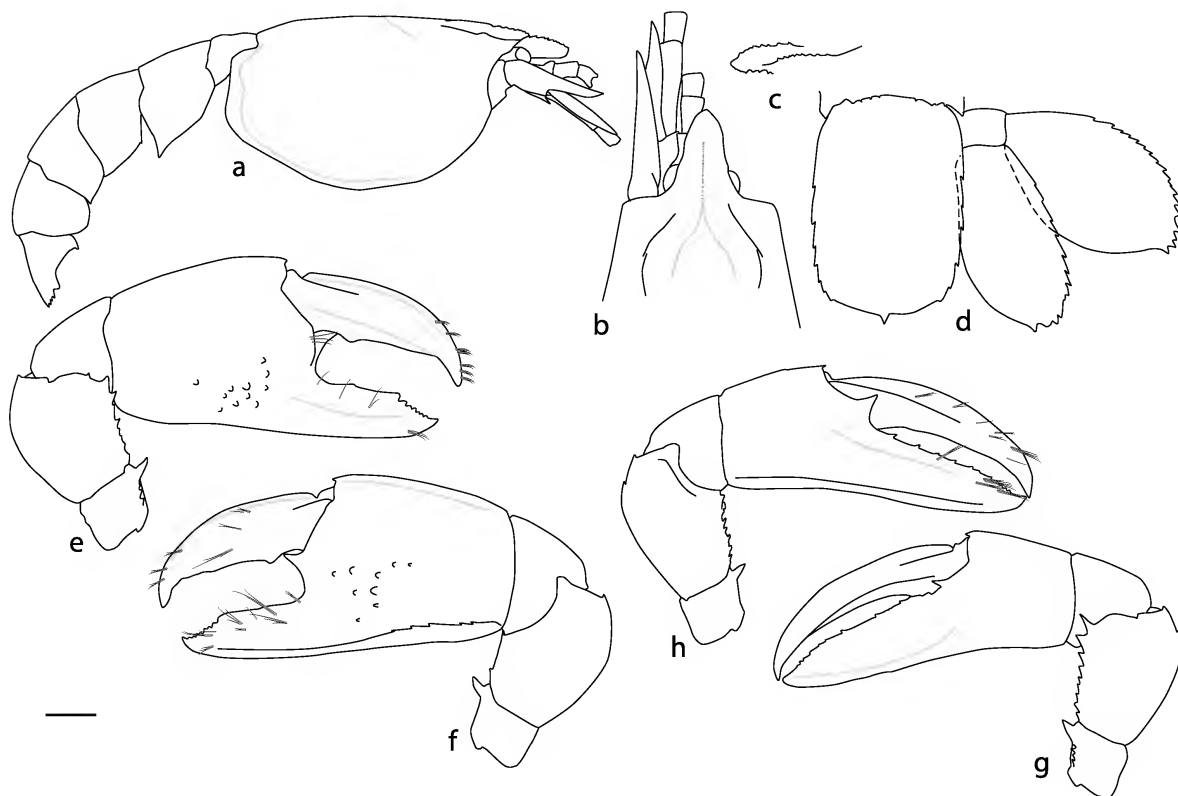
Eiconaxius crista-galli var. *antillensis* Bouvier, 1905: 803.*Iconaxius cristagalli* var. *antillensis*. – Balss, 1925: 210.*Axiis* (*Eiconaxius*) *crista-galli antillensis*. – Bouvier, 1925: 456–458, pl. 8 fig. 3, pl. 9 fig. 1. – De Man, 1925: 4, 33.*Eiconaxius antillensis*. – Sakai and de Saint Laurent, 1989: 21. – Kensley, 1996: 475. – Sakai, 2011: 273. – Felder et al. 2009: 1063.

Figure 1. *Eiconaxius antillensis* Bouvier, 1905, Syntype, MCZ 11964 (male, 6.1 mm) – a, carapace, pleon, lateral. b, anterior carapace, antenna, antennule, dorsal view. c, rostrum, anterior median carina, left oblique view. d, telson, right uropod. e, f, major cheliped (left), mesial, lateral views. g, h, minor cheliped (right), mesial, lateral views. Scale bar = 1 mm.

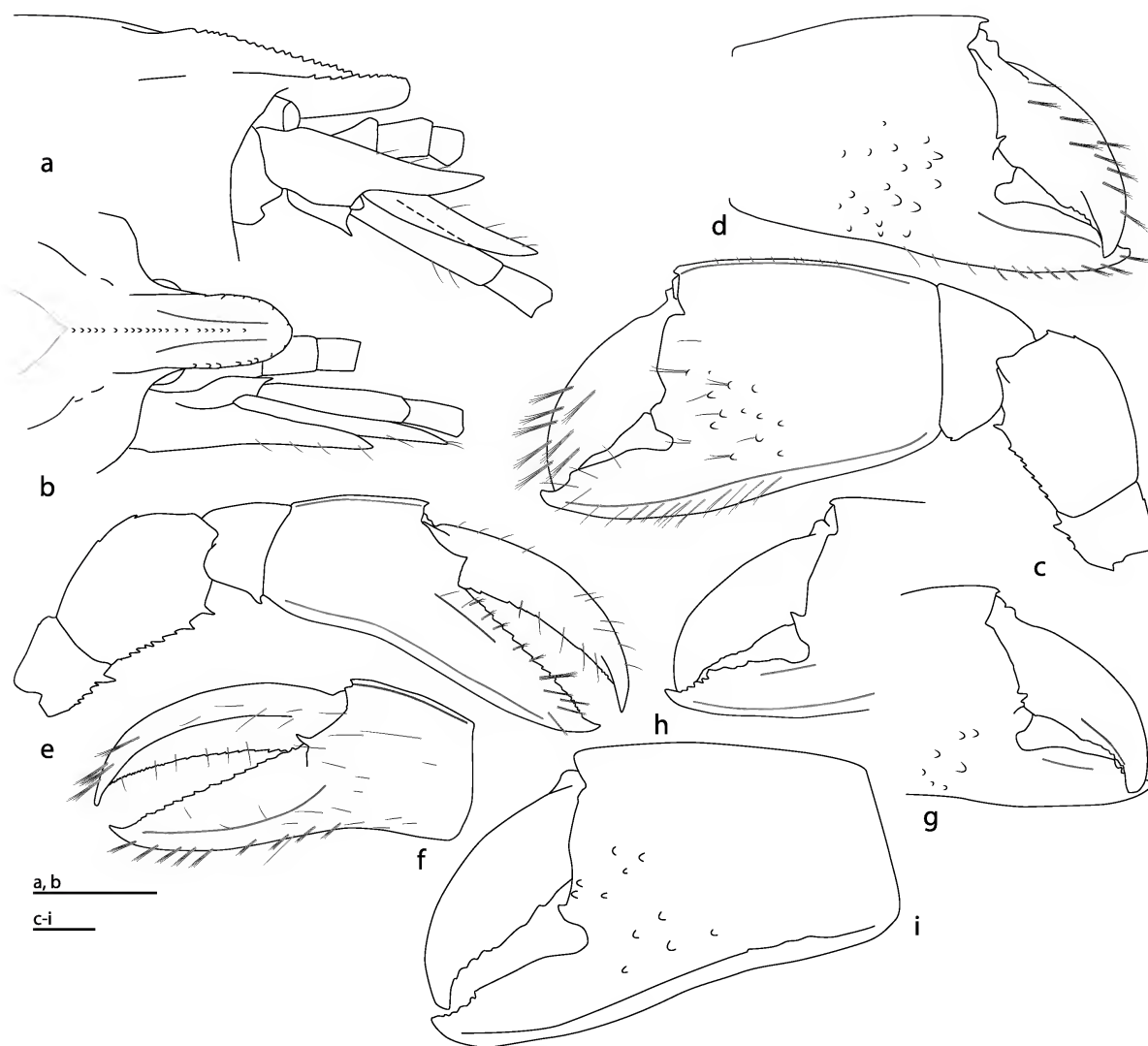


Figure 2. *Eiconaxius antillensis* Bouvier, 1905, IU-2016-8456 (ovigerous female, 6.3 mm) – a, b, anterior carapace, antenna, antennules, lateral, dorsal views. c, d, major cheliped (left), lateral, mesial views. e, f, minor cheliped (right), lateral, mesial views. g, h, major cheliped (left), distal propodus, dactylus, lateral, mesial views. NMV J71649 (ovigerous female, 7.6 mm) – i, major cheliped (left), lateral view. Scale bars = 1 mm.

Eiconaxius ?antillensis. – Poupin and Corbari, 2016: 32, fig. 8a (photograph).

Material examined. Syntypes. Off Montana, Monserrat, 16.7°N, 62.2°W, 545 m, Blake stn 154, MCZ CRU-11946 (male, 6.1 mm). Barbados, 12.9°N, 59.6°W, 527 m, Blake stn 281, MCZ CRU-11947 (ovigerous female, 6.7 mm).

Guadeloupe, N of Grande Terre, 16°37'N, 61°31'W, 432–482 m (KARUBENTHOS stn DW4550), MNHN IU-2016-8456 (ovigerous female, 6.3 mm), MNHN IU-2018-106 (3 females, 5.8–7.1 mm), MNHN IU-2013-18924 (2 males, 4.3, 6.7 mm), NMV J71649 (ovigerous female, 7.6 mm). NMV J71655 (4 females, 5.3–7.3 mm).

Caribbean Sea, Mexico, NE of Yucatan, 22.72°N, 86.22°W, 1030 m, (Cruise: 65A9-21) USNM 1014172 (1 specimen, det. B. Kensley, examined by C.C. Tudge). E of Guadeloupe, 16.55°N, 61.62°W, 466–585 m (Pillsbury stn P994), USNM 1081088 (3 specimens, examined by C.C. Tudge).

Diagnosis. Rostrum tapering more over distal third than proximal, with rounded apex in adult (acute in juvenile), 1.2–1.3 times as long as wide. Median carina erect, with clear dentition (10–20 teeth); lateral gastric carina with hiatus between lateral rostral margin and short gastric section, visible only posterior to confluence of submedian carinae. Major

cheliped, palm wider distally than at midpoint, distolateral margin with sharp tooth at base of finger; fixed finger about 3/4 length of upper margin of palm, cutting edge *with basal notch, blade-like proximal half, and distal concavity*; dactylus cutting edge *with blunt tooth at midpoint, denticulate beyond*. Minor cheliped, palm upper margin as long as greatest width; distolateral margin with prominent triangular toothed lobe at base of dactylus; fixed finger cutting edge weakly crenellate, with excavated distal quarter.

Distribution. Monserrat, Barbados, Guadeloupe, Caribbean Sea, W Atlantic, S. of Jamaica; 432–1030 m.

Remarks. Bouvier (1905) listed no specimens when he erected his new variety but mentioned a male and a female from two stations later (Bouvier, 1925). We treat them as syntypes. The male syntype differs significantly from all other specimens identified by us and by others in the past, including the second specimen identified by Bouvier (1925). Notably the distolateral margin of the palm of the major cheliped bears a high and sharp tooth (Fig. 1f) whereas in all other material there is a blunt asymmetrical tooth (Figs 2h, i are typical; broken in Fig. 2c). The notch below this tooth is less pronounced in the male syntype than in other specimens. These differences appear not size-related – this specimen is within the size range of the other material.

Eiconaxius antillensis is the only species of this group in the Atlantic but is confined to the Caribbean or nearby, an area with biogeographic affinities to the Indo-West Pacific where the remainder live. The species is similar to *E. cristagalli*, the Eastern Pacific species, in the dentition of the propodus and fixed finger of the major cheliped, both with a deep notch in the gape and a distal concavity on the finger. It differs in having a narrow, parallel-sided rostrum with numerous teeth on the median carina (cf. rostrum triangular, tapering, median carina with six or seven teeth in Faxon's and Kensley's accounts of *E. cristagalli*). Kensley (1996: fig. 7F) showed the distolateral margin of the minor cheliped of *E. cristagalli* with two teeth; only one is present on these specimens of *E. antillensis*. The lateral carina has a clear hiatus between the posterior extension of the rostral margin and the ridge level with the submedian carina, as in *E. gololobovi* sp. nov.; Kensley (1996) noted no such hiatus in *E. cristagalli*.

Eiconaxius asper Rathbun, 1906

Eiconaxius asper Rathbun, 1906: 895, fig. 52. – Sakai and de Saint Laurent, 1989: 22. – Kensley, 1996: 475. – Sakai, 2011: 273.

Iconaxius asper. – Balss, 1925: 209.

Axius (*Eiconaxius*) *asper*. – De Man, 1925: 4, 14, 34.

Diagnosis. Median carina erect, with clear dentition. *Major cheliped, palm wider distally than at midpoint. Major cheliped, palm lateral and mesial faces tuberculate near base of fingers*; distolateral margin *with 1 or 2 teeth in gape but without a deep notch*; fixed finger about half as long as upper margin of palm, cutting *with basal notch, blade-like proximal half, and distal concavity*; dactylus cutting edge with basal molar-like tooth, notch and straight beyond. Minor cheliped, palm lateral and mesial faces tuberculate near base of fingers.

Distribution. Hawaii, Kauai I., 418–628 fm (765–1149 m) (known only from type locality).

Remarks. Rathbun (1906) remarked that the species resembled *E. cristagalli* in having the median carina denticulate but differed in the 'presence of a larger basal tooth on dactylus of larger hand and a more prominent tooth not far from middle of the pollex [fixed finger]'. She illustrated only the larger cheliped where these differences are unconvincing compared to Faxon's (1895) figures of a type or Kensley's (1996) figure of *E. cristagalli* from the Galapagos. Without examining the types we are unsure of the status of this species. It is omitted from the key.

Eiconaxius cristagalli (Faxon, 1893)

Axius crista-galli Faxon, 1893: 193. – Faxon, 1895: 104, pl. 28 fig. 1–1h.

Axius (*Eiconaxius*) *crista-galli*. – Borradaile, 1903: 538. – De Man, 1925: 4, 14.

Eiconaxius crista-galli. – Rathbun, 1906: 895.

Iconaxius cristagalli. – Balss, 1925: 210.

Eiconaxius cristagalli. – Sakai and de Saint Laurent, 1989: 18. – Hendrickx, 1995: 390. – Hendrickx, 2008: 1002, fig. 2. – Kensley, 1996: 475, 480–481, fig. 7. – Sakai, 2011: 276–278.

Diagnosis. *Rostrum 1.5–2.0 times as long as wide. Median carina erect, with clear dentition.* Major cheliped, palm lateral and mesial faces tuberculate near base of fingers; distolateral margin *with single blunt tooth in gape*; fixed finger 0.6 length of upper margin of palm, cutting edge *with broad blade over proximal half, irregular beyond*; dactylus cutting edge with basal molar-like tooth, notch and straight beyond. Minor cheliped, palm upper margin as long as greatest width; distolateral margin with prominent bifid triangular tooth at base of dactylus. Uropod endopod anterolateral apex acute, with 1 or few small teeth.

Distribution. Pacific coast, Panama (*Albatross* stn 3358), 465 fm (851 m) (type locality); Ecuador, Galapagos Is, 717 m (Kensley, 1996), 1123–1378 m (Hendrickx, 2008).

Remarks. The species was redescribed by Kensley (1996) and compared by us with *E. antillensis* above. Hendrickx (2008) illustrated variation in the dentition of the rostrum of five syntypes and recorded the species from much greater depths than previously.

Eiconaxius dongshaensis sp. nov.

(<http://zoobank.org/urn:lsid:zoobank.org:act:7A965426-D789-4C02-8B8C-4A3A84C17E3B>)

Figures 3, 4a, b

Eiconaxius indicus. – Sakai and Ohta, 2005: 73–77, figs 3–5. – Tsang et al., 2008: 363, fig. 2.

Material examined. Holotype. South China Sea, off Pratas Islands, S of Hong Kong, 20°50.9'N, 117°27.17'E, 730–720 m (stn CD320), NTOU A01439 (female, 10.0 mm).

Paratype. Collected with holotype, NTOU A01440 (female, 9.4 mm).

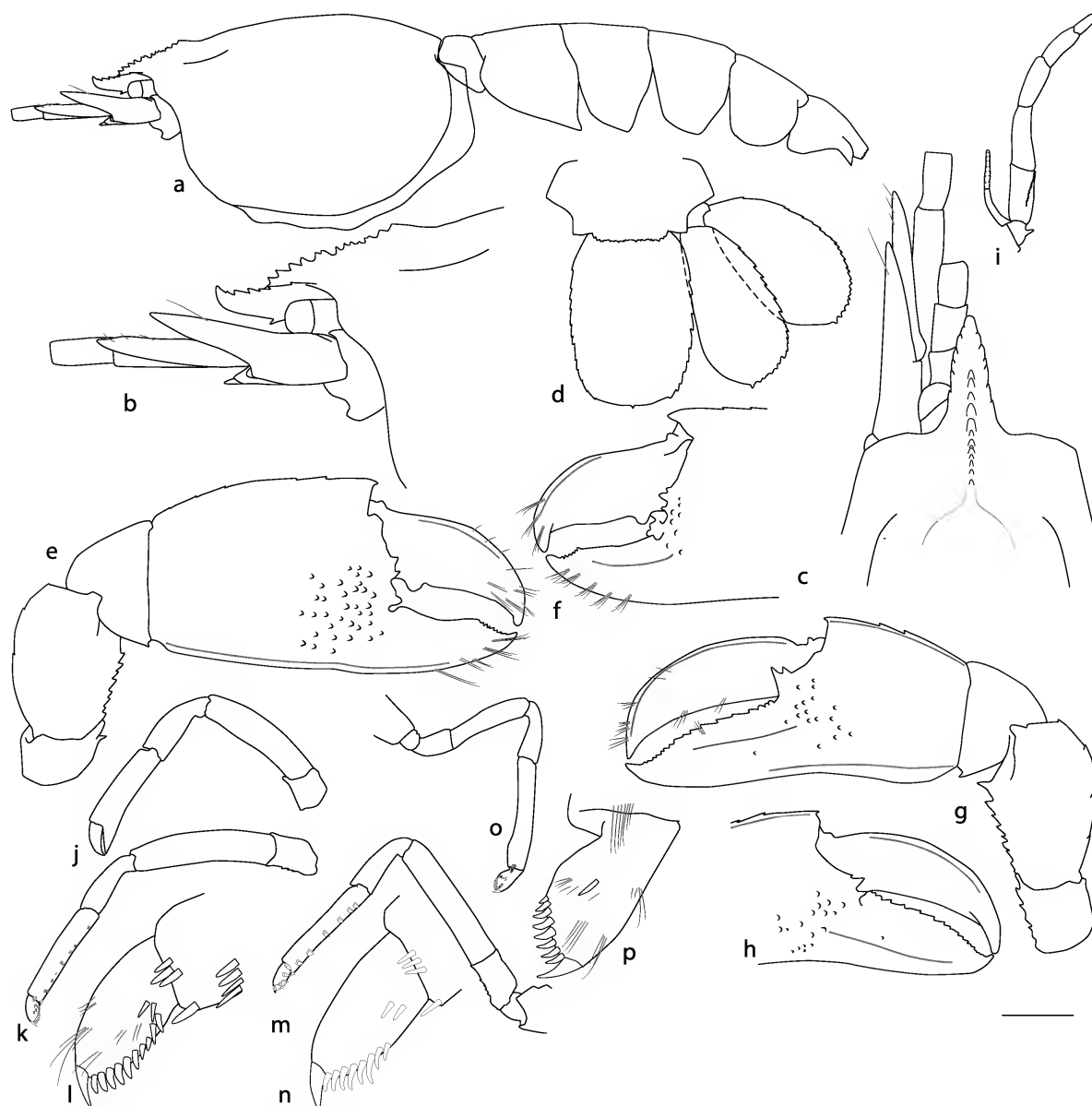


Figure 3. *Eiconaxius dongshaensis* sp. nov. Holotype, NTOU A01439 (female, 10.0 mm) – a, carapace, pleon, lateral. b, anterior carapace, antenna, lateral. c, anterior carapace, antennule, antenna, dorsal. d, pleomere 6, telson, right uropod. e, f, right major cheliped, lateral and mesial. g, h, left minor cheliped, lateral and mesial. i, maxilliped 3. j, pereopod 2. k, l, left pereopod 3, detail of dactylus. m, n, left pereopod 4, detail of dactylus. o, p, left pereopod 5, detail of dactylus. Scale = 2 mm (except b, c, l, n, p).

Diagnosis. Rostrum 1.5–2.0 times as long as wide; with ventral tooth. Median carina erect, with clear dentition; sublateral gastric carinae present, diverging widely from base of median carina; lateral gastric carina not running from rostrum, commencing level with confluence of submedian carinae. Major cheliped, palm wider distally than at midpoint, upper

margin denticulate; lateral and mesial faces of palm tuberculate near base of fingers; distolateral margin with 2 teeth at base of dactylus, lobe and keyhole-shaped notch in gape; fixed finger about half as long as upper margin of palm, cutting edge with basal notch, blade-like proximal half, and distal concavity; dactylus cutting edge with basal molar-like tooth, notch and

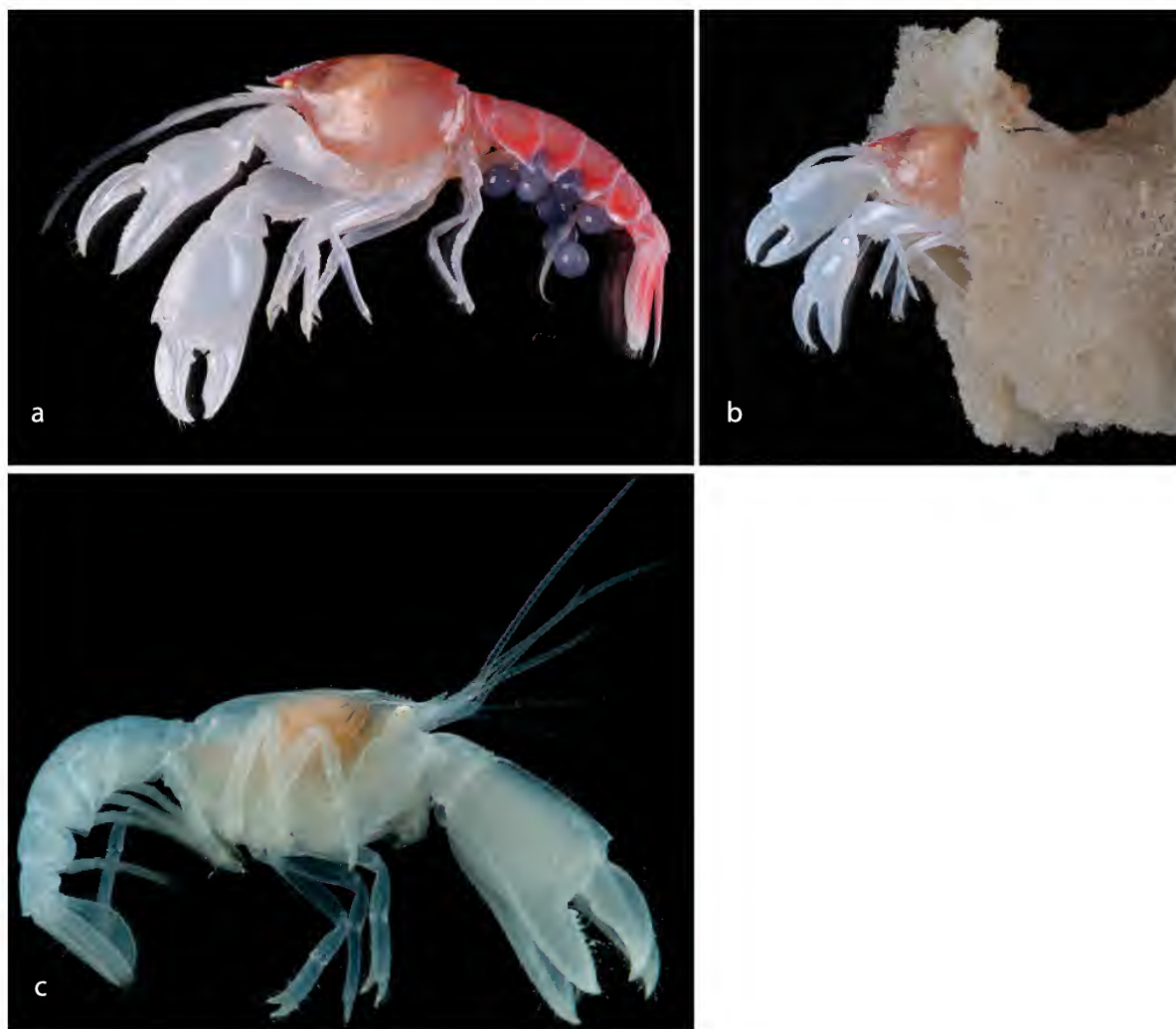


Figure 4. *Eiconaxius dongshaensis* sp. nov., holotype, NTOU A01439 (female, 10.0 mm) – a, habitus, in vivo. b, habitus in host sponge (photos, Tin-Yam Chan). *Eiconaxius gololobovi* sp. nov., unspecified specimen – c, habitus, in vivo (photo, David Shale).

straight beyond. Minor cheliped, palm upper margin as long as greatest width; distolateral margin with prominent triangular tooth at base of dactylus (bifid); lateral and mesial faces tuberculate near base of fingers.

Description. Carapace smooth. Rostrum 0.18 carapace length, concave dorsally, tapering evenly to acute tip, twice as long as wide at base, with 6 teeth on lateral margins, depressed below level of median carina, not continuous with lateral carinae, with ventral tooth. Lateral gastric carina unarmed, reaching anteriorly to base of median carina. Submedian gastric carina smooth, together curved and converging on median carina. Median gastric carina prominent, erect, reaching two-thirds along rostrum, with c. 13 uneven sharp teeth.

Pleuron 1 posteroventrally rounded; pleuron 2 truncate, posteroventrally acute; pleura 3 and 4 truncate, posteroventrally subacute; pleuron 5 rounded, all 5 pleura without anteroventral tooth; pleuron 6 with acute posteroventral angle; pleonite 6 dorsal posterior margin denticulate.

Eyestalk, 0.4 length of rostrum; cornea white. Antennular peduncle reaching to midpoint of antennal article 4; article 1 unarmed. Antennal peduncle article 1 unarmed; article 2 with upper-distal elongate triangular blade, reaching two-thirds along article 4; scaphocerite a vertical blade, reaching just beyond end of article 4; article 3 lower margin with distomesial tooth; article 5 about half length of article 4.

Maxilliped 3 basis with mesial spine; ischium unarmed; crista dentata of about 16 small similar teeth; merus and carpus unarmed; exopod with flagellum reaching to base of merus.

Major cheliped merus lower margin with c. 8 irregular teeth, upper margin with 2 minute blunt teeth; carpus lower margin with 1 distal tooth; propodus upper margin carinate, obscurely dentate, angled distally, length 0.9 greatest height, lower margin smooth, lateral face tuberculate near base of fixed finger, mesial face with few tubercles near base of fixed finger; fixed finger 0.6 times as long as upper palm, cutting edge shallowly concave over proximal two-thirds, denticulate beyond, with longitudinal mesial ridge; distolateral margin of palm with 2 teeth at base of dactylus, lobe and keyhole-shaped notch in gape; distomesial margin of palm with 2 teeth at base of dactylus; dactylus distally curved, upper margin carinate, cutting edge with basal tooth, straight beyond.

Minor cheliped shorter and more slender than major, palm 0.8 times height of major palm; merus lower margin with 8 sharp teeth, increasing in size distally; carpus lower margin with 1 distal tooth; propodus dilating, upper margin carinate, weakly denticulate, as long as greatest height, lower margin smooth, lateral and mesial faces tuberculate near base of fixed finger; fixed finger 1.25 times as long as upper palm, cutting edge dentate, with longitudinal mesial and lateral ridges; distolateral margin of palm oblique, with prominent bifid triangular tooth in gape; distomesial margin of palm oblique, with 2 triangular teeth in gape; dactylus distally curved, upper margin carinate, cutting edge smooth.

Pereopod 2 ischium lower margin unarmed; merus lower margin unarmed; carpus 0.8 length of propodus upper margin; propodus upper margin 2.5 times as long as dactylus. Pereopod 3 merus unarmed; propodus 3.3 times as long as dactylus, with 7 rows of spiniform setae, of 2–4 setae; dactylus spatulate, with 10 spiniform setae along oblique margin, plus unguis, 4 facial spiniform setae. Pereopod 4 similar to pereopod 3; propodus 3.5 times as long as dactylus, with 7 rows of spiniform setae, of 1–3 setae; dactylus spatulate, with 8 spiniform setae along oblique margin, plus unguis, and 2 facial spiniform setae. Pereopod 5 dactylus spatulate, with 8 spiniform setae along oblique margin, plus unguis, with 1 facial spiniform seta.

Uropodal endopod 1.9 times as long as wide, oval, anterior-distal margin with c. 20 evenly-spaced teeth, without longitudinal ridge. Uropodal exopod 1.7 times as long as wide, oval, anterior margin with many small irregular teeth over most of length, without longitudinal rib.

Telson 1.35 times as long as wide, widest at midlength, then tapering to rounded posterolateral angles, lateral margin upturned, denticulate, distal margin evenly curved, with posteromedian spine; dorsal face smooth, concave.

Etymology. *dongshaensis*, from Dongsha, the Chinese name of the Pratas Islands near the type locality.

Distribution. Sulu Sea, Philippines, 688–2019 m (Sakai and Ohta, 2005); Pratas Is., South China Sea, 720–730 m (Tsang et al., 2008).

Remarks. Sakai and Ohta (2005) illustrated the habitus, tailfan and chelipeds of this species as *Eiconaxius indicus* based on

nine specimens of both sexes from the Sulu Sea. Their figures can by-and-large be reconciled with those published here. The chelipeds are similar but the palmar distolateral and mesiolateral armature is simpler in their figures than in the types. Sakai and Ohta (2005) showed tubercles on the lateral face of the palm of the major cheliped in fig. 3 but not in fig. 5, and did not note the easily overlooked subrostral tooth.

Eiconaxius dongshaensis is the only species in this group with a rostral ventral tooth. This tooth and the small keyhole-shaped notch in the gape of the cheliped are like no other species.

Eiconaxius gololobovi sp. nov.

(<http://zoobank.org/urn:lsid:zoobank.org:act:6BA2620A-9AF9-4536-AD2F-4C0E980F65D8>)

Figures 4c, 5–8

Material examined. Holotype. SW Indian Ocean, Gololobov Bank, ‘Coral’ seamount, 41°21.0283’S, 42°55.145’E, 1117 m (RV *James Cook* cruise JC606, code 996) NHMW 25659 (female, 7.8 mm).

Paratypes. SW Indian Ocean, Gololobov Bank, ‘Coral’ seamount, 41°21.767’S, 42°54.907’E, 686.5 m, NHMW 25658 (male, 6.8 mm), NHMW 25660 (female, 6.1 mm), NHMW 25661 (male, 7.7 mm), NHMW 25662 (male, 5.1 mm), NHMW 25663 (female, 5.4 mm), NHMW 25664 (female, 6.8 mm), NHMW 25665 (male, 4.8 mm), NHMW 25666 (male, 8.3 mm), NHMW 25667 (ovigerous female, 9.1 mm), NHMW 25668 (ovigerous female, 8.1 mm), NHMW 25669 (male, 7.0 mm), NHMW 25670 (ovigerous female, 8.0 mm), NHMW 25671 (male, 6.2 mm), NHMW 25672 (male, 5.6 mm), NHMW 25673 (female, 5.6 mm), NHMW 25674 (ovigerous female, 8.8 mm), MNHN IU-2016-8156 (male, 7.4 mm), NMV J71648 (male, 7.8 mm), NHMW 26058 (male, 6.1 mm), NHMW 26059 (female, 6.8 mm).

Other material. Madagascar. S of Pt Barrow, 25°39’S, 44°16’E, 986–991 m (ATIMO VATAE stn CP3596), MNHN IU-2014-12083 (ovigerous female, 7.4 mm).

Mozambique Channel, Geyser Bank, between Malekula and Ambrym islands, 12°18’S, 46°27’E, 920–935 m (BIOMAGLO stn DW4791), MNHN IU-2017-530 (male, 6.4 mm).

Diagnosis. Rostrum parallel-sided proximally, with acute apex, 1.2–1.3 times as long as wide. Median carina erect, with clear dentition; sublateral gastric carinae present, diverging widely from base of median carina; lateral gastric carina continuous with short overlap of ridges posterior to confluence of submedian carinae. Major cheliped, merus lower margin with 2 spines near midpoint, or with single denticle; palm wider distally than at midpoint, upper margin smooth, carinate, or denticulate (juveniles); fixed finger about half as long as upper margin of palm, cutting edge crenellate, with row of diminishing rounded teeth; dactylus cutting edge smooth. Minor cheliped, palm upper margin significantly less than greatest width; distolateral margin with prominent triangular tooth at base of dactylus; fixed finger cutting edge smooth, straight.

Description of holotype. Carapace smooth, few obsolete tubercles on gastric region between carinae. Rostrum 0.18 carapace length, concave dorsally, tapering distally to acute tip, 1.35 times as long as wide at base, with c. 8 obscure teeth on lateral margins, depressed below level of median carina, continuous with lateral carinae, without ventral tooth. Lateral gastric carina unarmed, with posterior section weakly separated

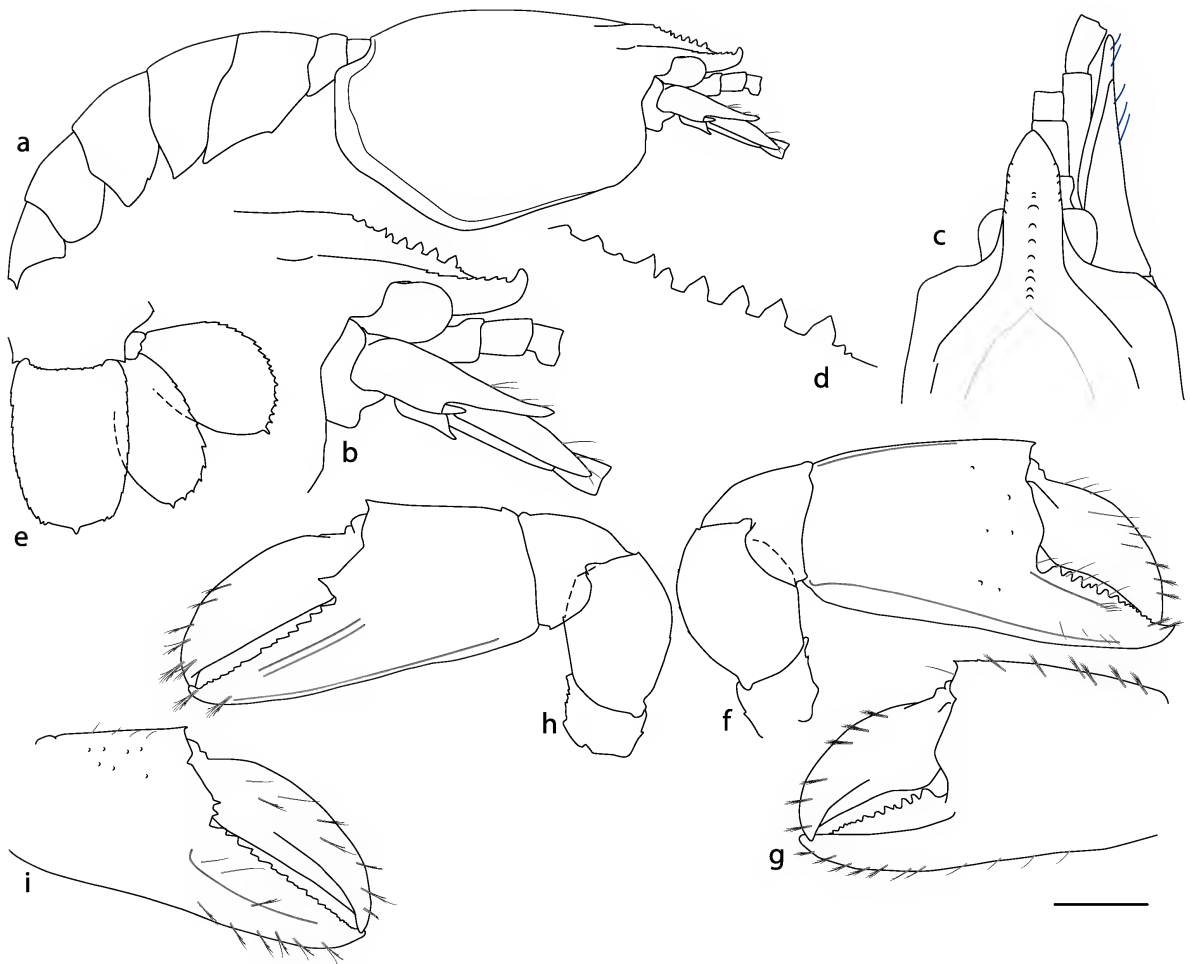


Figure 5. *Eiconaxius gololobovi* sp. nov., holotype, NHMW 25659 (male, 7.8 mm) – a, carapace, pleon, lateral. b, c, anterior carapace, antennule, antenna, lateral and dorsal. d, median carina. e, pleomere 6, telson, right uropod. f, g, right major cheliped, lateral and mesial. h, i, left minor cheliped, lateral and mesial. Scale bar = 1 mm (except b–d).

from, but almost overlapping anterior section. Submedian gastric carina smooth, together curved and converging on median carina, slightly longer than lateral gastric carina. Median gastric carina prominent, erect, reaching midpoint of rostrum, with 9 erect teeth becoming pentagonal anteriorly.

Pleuron 1 posteroventrally acute; pleura 2, 3 truncate, posteroventrally acute; pleuron 4 truncate, posteroventrally subacute, with anteroventral tooth; pleuron 5 rounded; pleuron 6 with acute posteroventral angle; pleonite 6 dorsal posterior margin denticulate.

Eyestalk, reaching half length of rostrum; cornea white. Antennular peduncle reaching two-thirds length of antennal article 4; article 1 unarmed. Antennal article 1 unarmed; article 2 with distal spine an elongate triangular blade, reaching two-thirds length of article 4; scaphocerite a

vertical blade, reaching to end of article 5; article 3 lower margin with distomesial tooth; article 5 about half length of article 4.

Maxilliped 3 coxa unarmed; ischium with tubercle; crista dentata of c. 15 similar obsolete teeth; merus and carpus unarmed; exopod reaching beyond midpoint of merus.

Major cheliped merus lower margin convex, with 3 minute teeth, upper margin with minute blunt tooth; carpus lower margin with 1 distal tooth; propodus upper margin carinate, angled distally, length 1.15 greatest height, lower margin smooth, lateral face with few minute tubercles; mesial face smooth; fixed finger 0.7 times as long as upper palm, cutting edge with proximal U-shaped notch, 10 diminishing triangular teeth, with longitudinal lateral ridge; distolateral margin of palm weakly evenly convex;

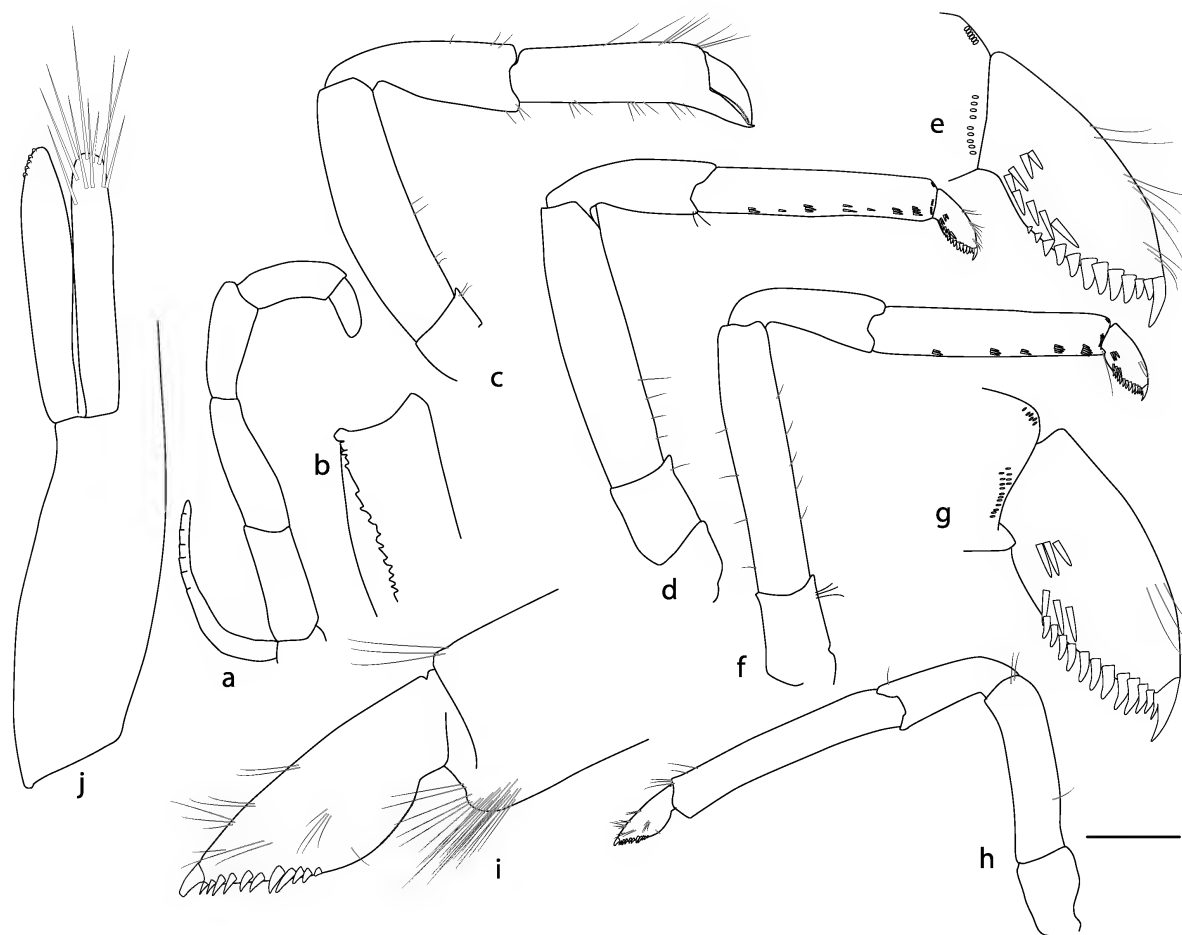


Figure 6. *Eiconaxius gololobovi* sp. nov., holotype, NHMW 25659 (male, 7.8 mm) – a, b, maxilliped 3, anterior detail of merus. c, pereopod 2. d, e, right pereopod 3, detail of dactylus. f, g, right pereopod 4, detail of dactylus. h, i, right pereopod 5, detail of dactylus. j, pleopod 2, proximal endopod, appendices interna and masculina. Scale = 1 mm (except b, e, g, i)..

distomesial margin of palm convex; dactylus distally curved, upper margin carinate, cutting edge smooth, weakly convex proximally.

Minor cheliped shorter and more slender than major, palm 0.9 times height of major palm; merus lower margin with minute tooth at midpoint; carpus lower margin with 1 distal tooth; propodus dilating, upper margin carinate, with obscure proximal notch, 0.85 times greatest height, lower margin smooth, lateral and mesial faces smooth; fixed finger 1.4 times as long as upper palm, cutting edge weakly serrate, with longitudinal lateral ridge; distolateral margin of palm oblique, with prominent triangular tooth in gape; distomesial margin of palm oblique-convex, with 2 tubercles in gape; dactylus distally curved, upper margin carinate, cutting edge smooth.

Pereopod 2 ischium lower margin unarmed; merus lower margin unarmed; carpus as long as propodus upper margin; propodus upper margin 2.2 times as long as dactylus. Pereopod 3 merus unarmed; propodus 2.8 times as long as dactylus, with 5 rows of 1–4 spiniform setae; dactylus spatulate, with 11 spiniform setae along oblique margin, plus unguis, and 2 rows of 3 facial spiniform setae. Pereopod 4 merus more slender than that of pereopod 3; propodus 2.8 times as long as dactylus, with 6 rows of 2–5 spiniform setae; dactylus spatulate, with 12 spiniform setae along oblique margin, plus unguis, and 2 oblique rows of 3 facial spiniform setae. Pereopod 5 dactylus spatulate, with 11 spiniform setae along oblique margin, plus unguis, without facial spiniform seta.

Pleopod 2 with appendices interna and masculina of similar lengths, 0.8 length of proximal endopod. Uropodal endopod 1.9

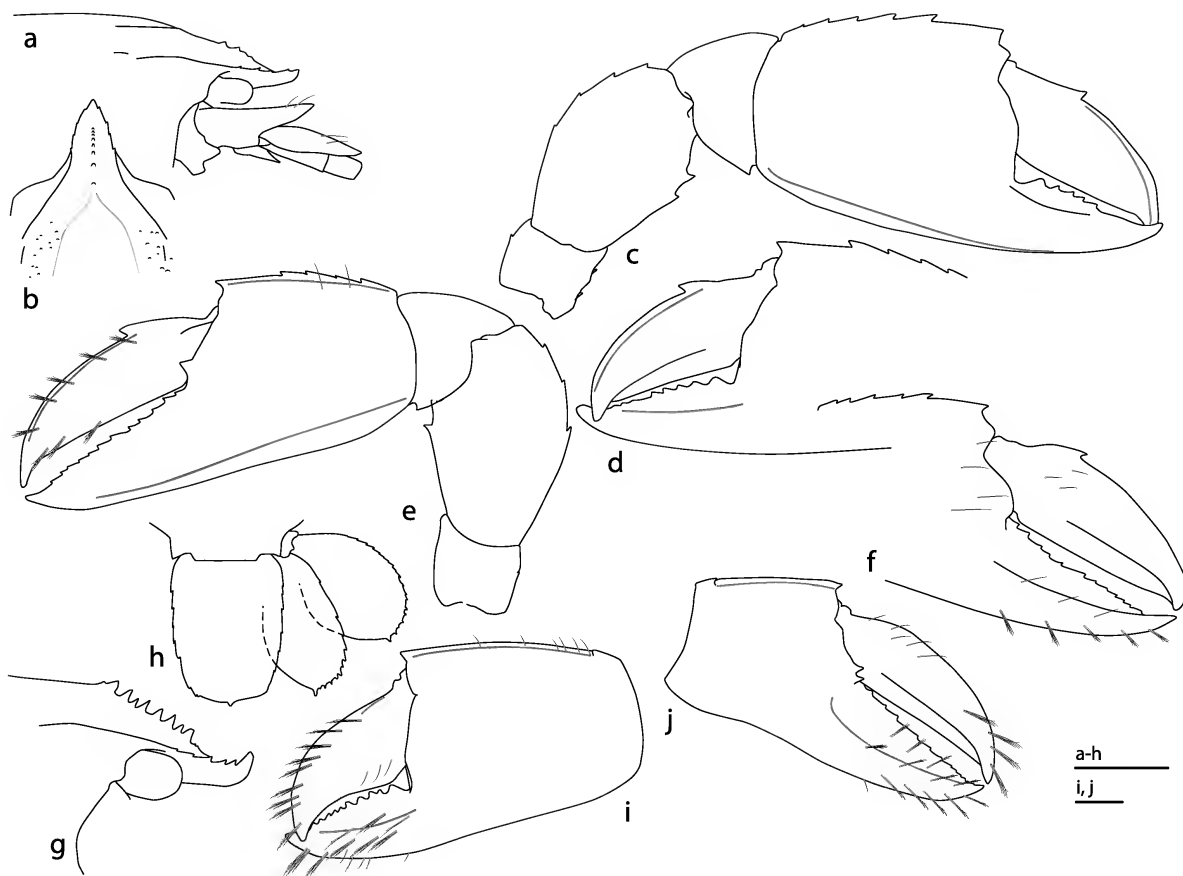


Figure 7. *Eiconaxius gololobovi* sp. nov., NHMW 25662 (male, 5.1 mm) – a, anterior carapace, antenna, lateral. b, anterior carapace, dorsal. c, d, right major cheliped, lateral and mesial. e, f, left minor cheliped, lateral and mesial. NHMW 25658 (male, 6.8 mm) – g, anterior carapace. h, pleomere 6, telson, right uropod. i, left major cheliped, j, right minor cheliped. Scales = 1 mm.

times as long as wide, oval, anterior-distal margin with 10 evenly-spaced teeth, last distal, without longitudinal ridge.

Uropodal exopod 1.4 times as long as wide, oval, anterior margin with small irregular teeth over distal two-thirds, without longitudinal rib.

Telson 1.5 times as long as wide, widest at third length, then tapering to posterolateral angles, lateral margin upturned, obscurely denticulate, distal margin obtusely angled, with posteromedian spine; dorsal face smooth.

Etymology. For Ya. K. Gololobov (1909–1980), Russian oceanographer, for whom the Gololobov Bank on the South-west Indian Ocean Ridge is named, of which the type locality, ‘Coral’ seamount, is part.

Distribution. Gololobov Bank, Mozambique Channel, south-west Indian Ocean; 686–1117 m depth.

Remarks. *Eiconaxius gololobovi* sp. nov. is known from 21 specimens ranging 4.8–9.1 mm in carapace length collected from

sponges by ROV on the Gololobov Bank, plus two from nearby localities in the Mozambique Channel. The species is distinguished from others in this group by the regularly dentate cutting edge of the fixed finger of the major cheliped (simple in other species) and from most species by the hiatus in the lateral carina. The dentition of cheliped fingers is obsolete in the ovigerous female from Madagascar (Fig. 8l, m). This individual has a more acute rostrum than others (Fig. 8i) but in this is similar to at least one smaller male (Fig. 8b) from Mozambique Channel. While several individuals display the distinctive pentagonal teeth on the median carina (Fig. 5d) (like children’s drawings of little houses), others have a similar number of more irregular teeth (Figs 7g, 8a, h) but in the smallest specimen dentition is obsolete (Fig. 7a). The upper margin of the propodus of the chelipeds often has a clear proximal notch (Figs 5h, i, 7i, j) but it is not obvious on the major cheliped of larger individuals (Figs 5f, g, 8d, e, l). The smallest individuals differ in having this margin serrate and a prominent tooth on the upper margin of the dactylus (Figs 7c–f).

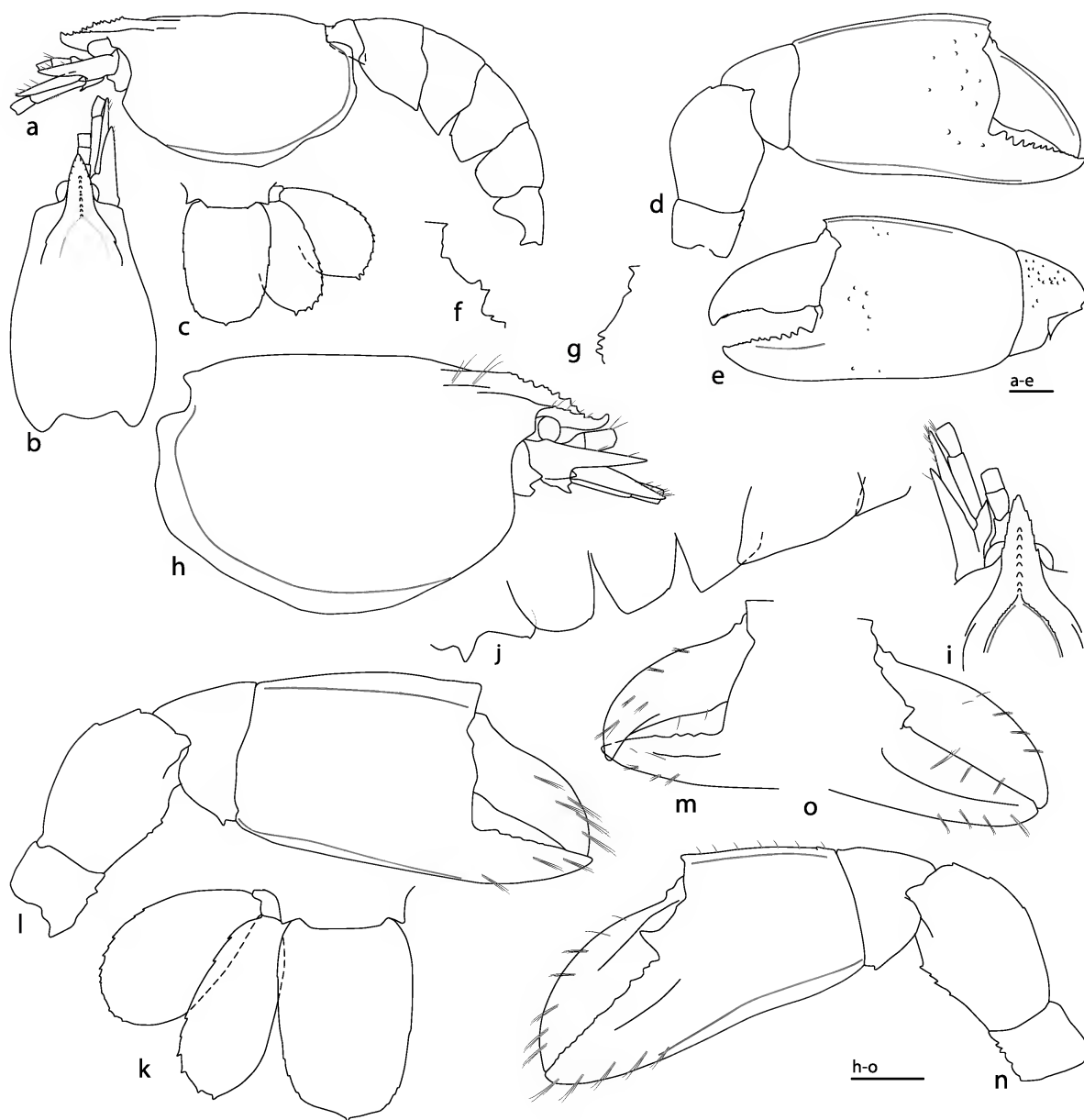


Figure 8. *Eiconaxius gololobovi* sp. nov., MNHN IU-2013-7046 (male, 6.4 mm) – a, carapace, pleon, lateral. b, carapace, dorsal. c, pleomere 6, telson, right uropod. d, e, right major cheliped, lateral and mesial. NMV J71648 (male, 7.8 mm) – f, right minor cheliped, propodus distolateral margin. MNHN IU-2016-8156 (male, 7.4 mm) – g, right minor cheliped, propodus distomesial margin. MNHN IU-2014-12083 (ovigerous female, 7.4 mm) – h, carapace, antennule, antenna, lateral. i, carapace, antennule, antenna, dorsal. j, right epimera of pleomeres 1–6. k, pleomere 6, telson, left uropod. l, m right major cheliped, lateral and mesial. n, o, left minor cheliped, lateral and mesial. Scale bars = 1 mm.

***Eiconaxius indicus* (De Man, 1907)**

Figures 9, 10

Iconaxius crista-galli var. *indica* De Man, 1907: 128–129.*Iconaxius cristagalli* var. *indica*. – Balss, 1925: 210.*Axius* (*Eiconaxius*) *crista-galli* var. *indica*. – De Man, 1925: 4, 15, 31, pl. 2 fig 3.*Eiconaxius indica*. – Sakai and de Saint Laurent, 1989: 22.*Eiconaxius indicus*. – Kensley, 1996: 475. – Sakai, 2011: 279

(partim), fig. 52.

Not *Eiconaxius indicus*. – Sakai and Ohta, 2005: 73–77, figs 3–5.
– Tsang et al., 2008: 363, fig. 2 (= *Eiconaxius dongshaensis* sp. nov.)**Material examined.** Holotype. Indonesia, E of Palau Kei Besar (Great Kei I.), 5°54'S, 132°56'7"E, 984 m (*Siboga* stn 267), ZMA102465 (ovigerous female, 10.6 mm) – photographed by C.H.J.M. Fransen, figured by Sakai (2011: fig. 52).

Vanuatu. Between Malekula and Ambrym islands, 16°30.7'S, 167°55.5'E, 550–565 m (BOA1 stn CP2468), MNHN IU-2014-10474

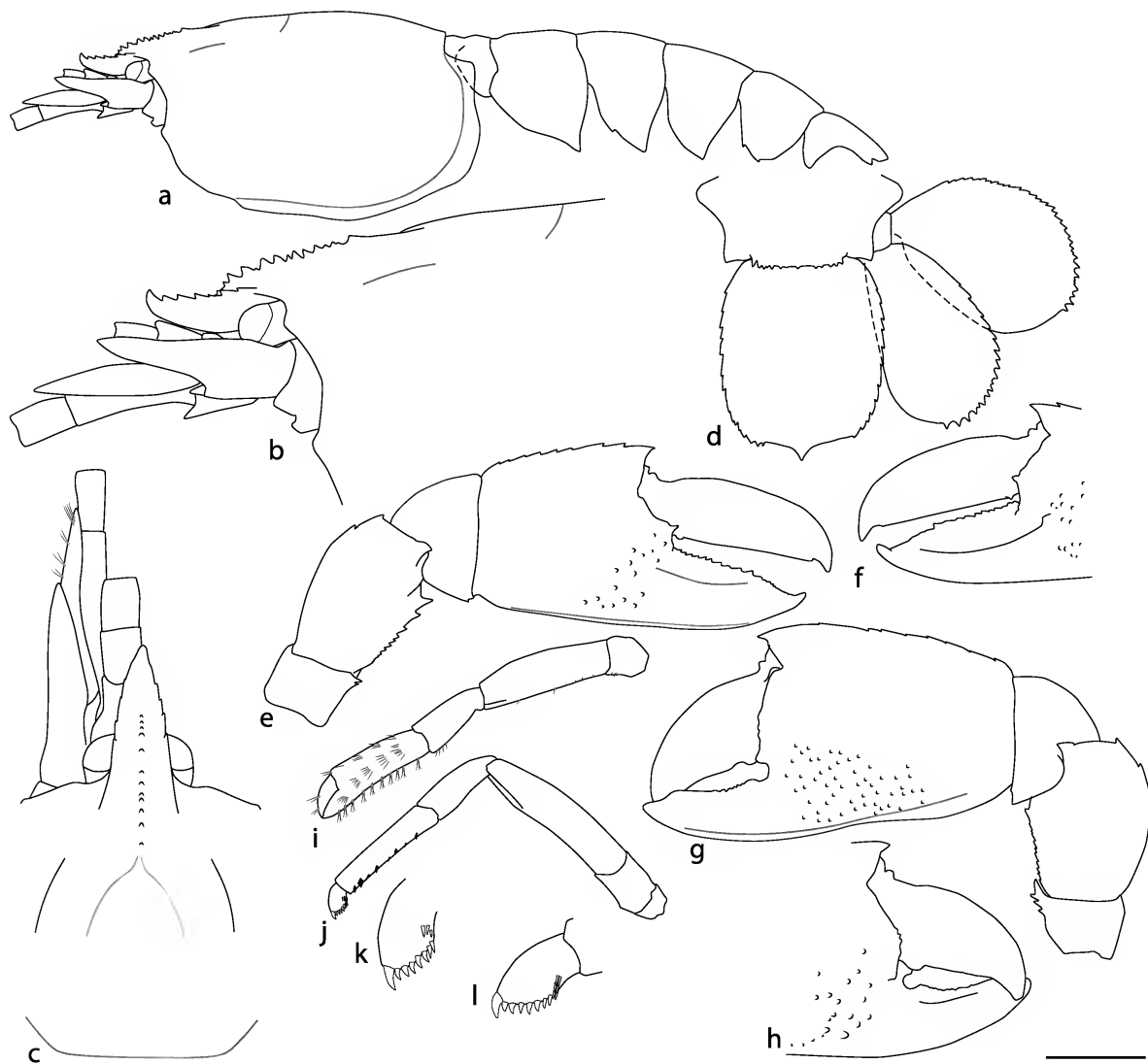


Figure 9. *Eiconaxius indicus* (De Man, 1907). MNHN IU-2014-10474 (male, 9.1 mm) – a, carapace, pleon, lateral. b, anterior carapace, antenna, lateral. c, anterior carapace, antennule, antenna, dorsal. d, pleomere 6, telson, right uropod. e, f, right minor cheliped, lateral and mesial. g, h, left major cheliped, lateral and mesial. i, pereopod 2. j, k, left pereopod 3, detail of dactylus. l, left pereopod 5, detail of dactylus. Scale = 2 mm (except b, c, k, l).

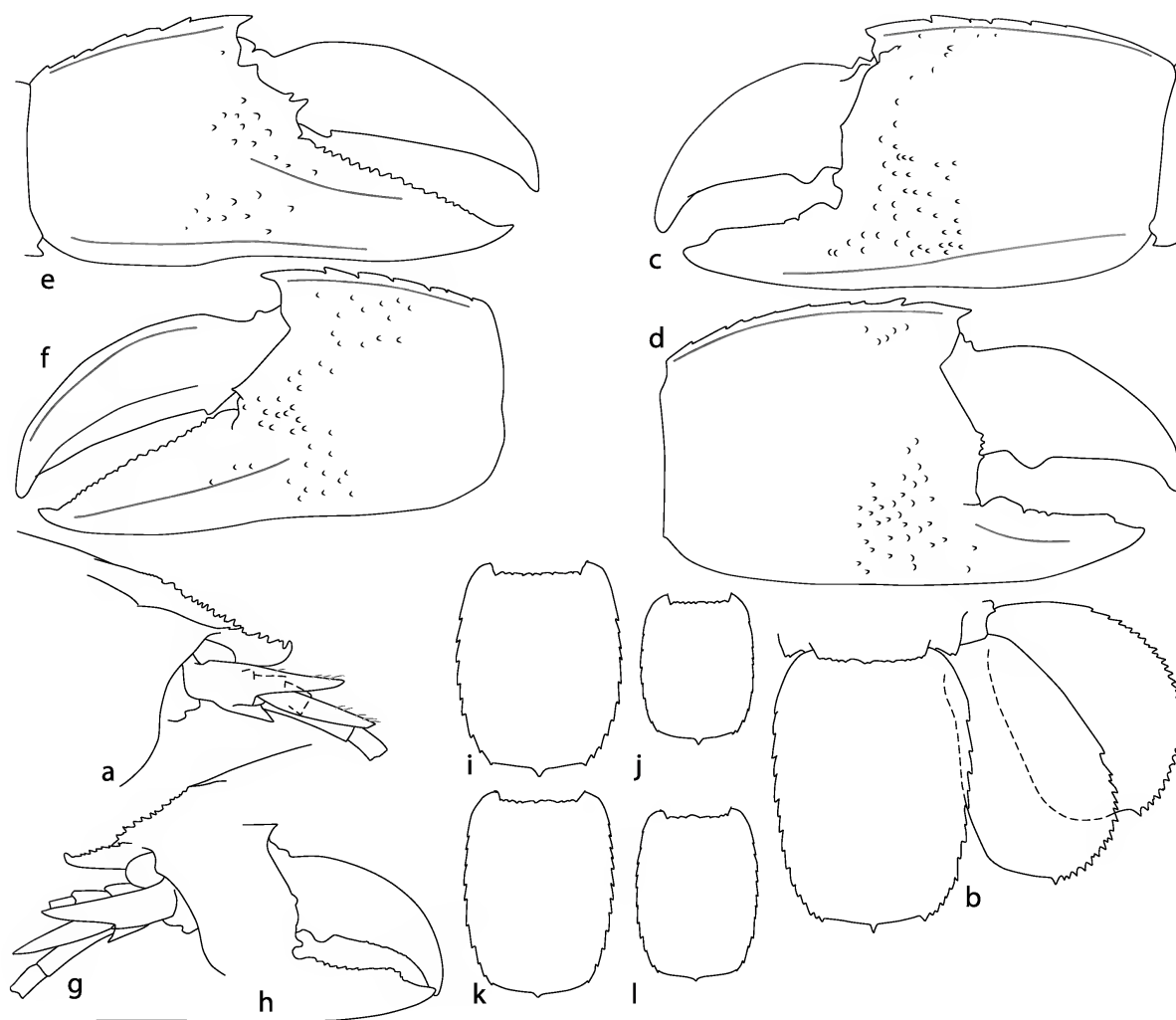


Figure 10. *Eiconaxius indicus* (De Man, 1907). MNHN IU-2016-8020 (ovigerous female, 12.1 mm) – a, anterior carapace, antenna. b, telson, right uropod. c, d, left major cheliped, lateral and mesial views. e, f, left minor cheliped, lateral and mesial views. MNHN IU-2014-7149 (ovigerous female, 11.0 mm) – g, anterior carapace, antenna. MNHN IU-2014-7151 (male, 9.0 mm) – h, right major cheliped fingers, lateral view. NMV J71631 – telsons of 4 individuals: i, male, 9.8 mm; j, male, 7.3 mm; k, ovigerous female, 9.0 mm; l, female, 7.6 mm. Scale = 2 mm

(male, 9.1 mm). Between Malekula and Epi islands, 16°38.28'S, 167°58.38'E, 586–646 m (BOA0 stn CP2307), MNHN IU-2014-7149–7152 (2 ovigerous females, 10.8, 11.0 mm; 2 males, 9.0, 10.8 mm)

Solomon Islands, NW of San Cristobal, 09°56'S, 161°04'E, 418–432 m (SALOMON 1 stn DW1826), MNHN IU-2016-8020 (ovigerous female, 12.1 mm).

New Caledonia, BATHUS 3 stations. Loyalty Ridge, seamount K, 24°43'S, 170°07'E, 750–760 m (stn DW778), NMV J71631 (4 males, 6.1–9.8 mm; 3 females, 7.6–9.0 mm); seamount K, 24°44'S, 170°08'E, 770–830 m (stn DW776), MNHN IU-2016-8022 (2 females, 6.1, 9.3 mm); seamount D, 23°35'S, 169°37'E, 655 m (stn DW800), MNHN IU-2016-8023 (female, 10.0 mm). S of Ile des Pins, 23°09'S, 167°11'E, 650–680 m (BIOCAL stn DW36), MNHN IU-2016-8021 (female, 7.8 mm).

Diagnosis. Rostrum tapering more over distal third than proximal, with rounded apex in adult (acute in juvenile), 1.5–2.0 times as long as wide. Median carina erect, with clear dentition; sublateral gastric carinae present, diverging widely from base of median carina; lateral gastric carina with hiatus between lateral rostral margin and short gastric section, visible only posterior to confluence of submedian carinae. Major cheliped, palm upper margin smooth, carinate, or denticulate; lateral and mesial faces tuberculate near base of fingers; distolateral margin with 1 or 2 teeth in gape but without a deep notch; fixed finger about half as long as upper margin of palm, cutting edge

blade-like, with proximal notch and distal concavity; dactylus cutting edge with basal molar, notch and straight beyond. Minor cheliped, palm upper margin as long as greatest width; distolateral margin with sharp spine at base of dactylus; lateral and mesial faces *tuberculate near base of fingers*; fingers almost as long to longer than upper margin of palm.

Description. (based on MNHN IU-2014-10474, male, 9.1 mm). Carapace smooth. Rostrum 0.2 carapace length, concave dorsally, tapering evenly to acute tip, twice as long as wide at base, with c. 7 teeth on lateral margins, depressed below level of median carina, separated from lateral carinae by long hiatus, without ventral tooth. Lateral gastric carina visible only posterior to confluence of submedian carinae, short, unarmed. Submedian gastric carina smooth, together curved and converging on median carina. Median carina prominent, erect, reaching two-thirds along rostrum, with c. 12 uneven teeth. Pleuron 1 posteroventrally rounded; pleura 2, 3 posteroventrally produced, acute; pleura 4, 5 less produced, posteroventrally acute; pleura 3, 5 with anteroventral tooth; pleuron 6 with rounded posteroventral angle; pleonite 6 dorsal posterior margin denticulate.

Eyestalk third length of rostrum; cornea unpigmented. Antennular peduncle reaching to midpoint of antennal article 4; article 1 unarmed. Antennal article 1 unarmed; article 2 without distomesial spine, stylocerite an elongate triangular blade, reaching just beyond midpoint of article 4; scaphocerite a vertical blade, reaching midpoint of article 5; article 3 lower margin with mesial tooth; article 5 about half length of article 4.

Major cheliped ischium lower margin produced as spinose ridge; merus lower margin finely denticulate, upper margin with minute tooth; carpus lower margin with 1 distal tooth; propodus upper margin carinate, denticulate, toothed distally, length 1.25 greatest height, lower margin smooth, lateral face tuberculate on lower palm, mesial face tuberculate at base of fixed finger; fixed finger half as long as upper palm, cutting edge concave with proximal and subdistal obtuse teeth, with longitudinal mesial ridge; distolateral margin of palm denticulate, with blunt tooth above circular gape; distomesial margin of palm denticulate, angled tooth near gape; dactylus distally curved, cutting edge with blunt proximal tooth, otherwise straight, smooth.

Minor cheliped shorter and more slender than major, palm 0.9 times height of major palm; ischium lower margin with 2 subdistal spines; merus lower margin denticulate, most distal spine-like; carpus lower margin with 1 distal tooth; propodus dilating, upper margin carinate, denticulate, 0.95 times greatest height, lower margin smooth, lateral and mesial faces tuberculate at base of fixed finger; fixed finger as long as upper palm, cutting edge denticulate, with longitudinal mesial and lateral ridges; distolateral margin of palm oblique, with sharp spine in gape; distomesial margin of palm oblique, with spine in gape; dactylus almost straight, upper margin carinate, cutting edge smooth, with subdistal notch.

Pereopod 2 ischium lower margin unarmed; merus lower margin unarmed; carpus 0.85 length of propodus upper margin; propodus upper margin twice as long as dactylus. Pereopod 3 merus unarmed; propodus 3.0 times as long as

dactylus, with 9 rows of spiniform setae, of 2–4 setae; dactylus spatulate, with 7 spiniform setae along oblique margin, plus unguis, 3 facial spiniform setae. Pereopod 4 virtually identical to pereopod 3. Pereopod 5 propodus with 8 rows of spiniform setae; dactylus spatulate, with 6 spiniform setae along oblique margin, plus unguis, 6 facial spiniform setae.

Uropodal endopod 1.6 times as long as wide, elongate-oval, anterior-distal margin with 19 evenly-spaced teeth, last 3 teeth distal, without longitudinal ridge. Uropodal exopod 1.4 times as long as wide, oval, anterior margin with c. 30 small teeth over most of length, without longitudinal rib.

Telson 1.1 times as long as wide, widest at mid-length, tapering to square posterolateral angles, lateral margin upturned, denticulate, distal margin concave each side of posteromedian spine; dorsal face smooth.

Distribution. Indonesia, Solomon Is, New Caledonia, Vanuatu; 418–984 m.

Remarks. The holotype, photographed for us by Charles Fransen, clearly shows the uneven row of c. 15 teeth on the median carina, the short separate lateral carina on the right side, two prominent teeth on the distomesial margin of the propodus of the minor cheliped, the semi-enclosed notch at the base of the fixed finger with two irregular teeth above, and the obscurely denticulate blade on the distomesial margin of the propodus of the major cheliped. The marginal denticulation of the fingers and the tuberculation of the propodus are consistent with the present material. Sakai's (2011) figure 52 is consistent with this except for the absence of the lateral carina.

The circular notch in the gape of the propodus of the major cheliped is similar to that in *E. dongshaensis* sp. nov. but not as enclosing; *E. indicus* lacks the ventral rostral tooth seen in the new species.

The lateral gastric carina may be obvious (Fig. 10a) but typically displays a strong hiatus between the lateral rostral ridge (Fig. 9a–c) and is sometimes absent, especially in larger specimens (Fig. 10g). In males, the circular notch in the gape of the major cheliped sometimes appears almost keyhole-shaped. The specimens from New Caledonia exhibit some variability that includes that of the Vanuatu material. The telson has the same general appearance but ranges from 1.1 to 1.3 times as long as wide, males being broader than females (cf. Figs 9d, 10i, j with 10b, k, l). The armature of the distolateral margins of the chelipeds also varies, some more spinose than others.

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